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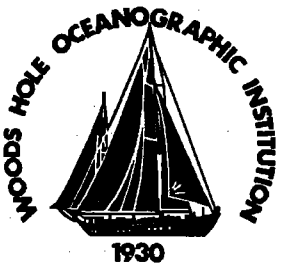

A Systematic Approach to Measuring the Social Behavior of Bottlenose Dolphins

by

Amy Samuels

September 1996

Technical Report

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Woods Hole, Massachusetts 02543

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Funding was provided by the Chicago Zoological Society, the Dolphins of Shark Bay Research Foundation, the National Oceanic and Atmospheric Administration through Contracts No. 40AANF200358, 40AANF201454, 40AANF201453 and by the Office of Naval Research through Contract N00014-93-1-1181.

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A SYSTEMATIC APPROACH TO MEASURING THE SOCIAL BEHAVIOR OF BOTTLENOSE DOLPHINS

By

Amy Samuels

B.S., University of California at Davis
1979

M.S., University of California at Davis
1982

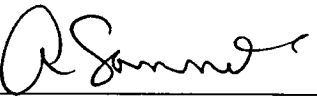
Submitted in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

at the

WOODS HOLE OCEANOGRAPHIC INSTITUTION

September 1996

Signature of Author: 

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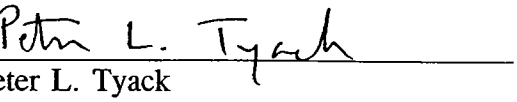
Certified by: 

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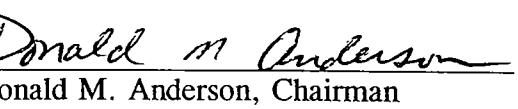
Accepted by: 

Donald M. Anderson, Chairman
Doctoral Degree Program Committee

For Peggy and Harold Samuels,
parents, scholars, and my source of inspiration

A SYSTEMATIC APPROACH TO MEASURING THE SOCIAL BEHAVIOR OF BOTTLENOSE DOLPHINS

by

Amy Samuels

Submitted in partial fulfillment of the requirements for the
Degree of Doctor of Philosophy at the Woods Hole Oceanographic Institution.

ABSTRACT

Cetacean biology is at a turning point with respect to studies of social behavior, a time of transition from anecdotal, descriptive natural history to focused, quantitative analyses of the social behavior of whales, dolphins, and porpoises. In my thesis, I seek to expedite this transition in several ways. The first chapter is primarily about the cultural, or historical, factors that have contributed to the methods of studying behavior and the ways of thinking about behavior that are idiosyncratic to cetacean biologists. In subsequent chapters, I seek to demonstrate the effectiveness of systematic methodologies for a better understanding of the social behavior and social relations of bottlenose dolphins.

In Chapter 1, I provide an intellectual history of studying cetacean social behavior. Behavioral studies of cetaceans come from a very different background than such studies of terrestrial mammals, with a unique set of terminologies, methodologies, and emphases. Beginning with the hunting tales of the early whaler-naturalists, this synthetic review describes the attempts to infer behavior and social structure from studies of whale carcasses; the intimate observations of small cetaceans at early oceanaria; the pseudo-scientific explorations of human-dolphin communication; the decline of zoo-based research on cetacean social behavior; the evolution of present-day, long-term field studies; and the all-pervasive influence of population biology. The review reveals that much of the groundwork has, in fact, been laid for the necessary next step: focused, quantitative studies of cetacean social behavior.

In Chapter 2, Samuels and Gifford investigated the agonistic behavior of bottlenose dolphins at Brookfield Zoo, using a quantitative technique adapted from primate behavioral research to determine dolphin dominance relationships. Dominance relations among dolphins were influenced by the gender of participants. Male dolphins were clearly and consistently dominant to females, and intersexual agonism occurred at moderate rates with seasonal peaks in spring and fall. Dominance relationships among female dolphins were age-ordered and stable, even though agonism among females occurred at uniformly low rates. In contrast, the two males had a changeable dominance relationship in which periods of stability and low-level agonism were interspersed with

episodes of intense competition. Research in a captive setting facilitated development of a quantitative technique that can be used to assess dominance relationships of wild dolphins. Zoo-based research also revealed patterns of behavior that conformed to current knowledge about societies of wild dolphins and generated predictions about the behavior of wild dolphins that can be tested using this technique.

In Chapter 3, Samuels, Richards, and Mann investigated the association of wild juvenile bottlenose dolphins with their mothers. Female juvenile bottlenose dolphins continued to associate with their mothers for several years following weaning. In contrast, juvenile sons rarely spent time with their mothers after independence even though they apparently remained in the same general area. Preliminary results suggested that the broader social network of juvenile males may be quite different from that of their female counterparts. In particular, sex differences in the social associations of juvenile dolphins appeared to foreshadow their adult social networks.

In Chapter 4, Samuels and Spradlin applied quantitative behavioral sampling techniques to a management concern, evaluation of the behavior of dolphins in Swim-With-Dolphin programs. Dolphin behavior in four captive programs was compared by the type of Swim encounter, defined by the presence ("Controlled") or absence ("Not-Controlled") of explicit trainer regulation of interactions between dolphins and human swimmers. Dolphin-swimmer interactions involving aggressive, submissive, or sexual behavior were designated as "high-risk" when humans were swimming with dolphins; sexual behavior was included as high-risk based on analyses that demonstrated co-occurrence of sexual and agonistic behaviors. High-risk activity comprised a substantial proportion of dolphin-swimmer social activity during Not-Controlled Swims. In contrast, high-risk activity rarely occurred during Controlled Swims, even though agonistic and sexual behaviors were normal components of the same dolphins' free-time social repertoire with other dolphins. These results indicated that direct trainer control of dolphin-swimmer interactions virtually eliminated high-risk activity from the Swim context, and thereby diminished the potential for dolphin distress, swimmer injury, and rejection of dolphins from Swim programs due to swimmer injury.

These studies of bottlenose dolphins illustrate the contributions of quantitative behavioral sampling techniques and complementary studies in captivity and in the wild for a better understanding of the social behavior and social relationships of cetaceans.

Thesis supervisor: Peter Lloyd Tyack, Associate Scientist

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I thank all the members of my committee for their support, friendship, and good advice. I especially thank Peter Tyack and Bill Watkins who welcomed me into their labs as a colleague and provided the combination of freedom and guidance that I needed to find my niche in cetacean biology. Peter Tyack deserves special mention for patience and support above and beyond the call of duty, as exemplified in his unwavering encouragement even when I contemplated switching to elephants after my original dissertation project fell through. Bill Watkins provided me with incredible experiences as a member of his sperm whale research team, including the opportunity to observe behavior on a very large scale. Aleta Hohn provided a common-sense sounding board on topics ranging from the evolution of life histories to swimming with dolphins, and set a model of scientific excellence for me to try to emulate. Janet Mann has been a long-time friend and co-conspirator in the crusade to instill systematic sampling techniques into studies of cetacean social behavior. Judy McDowell, the chair of my committee, kept our discussions on track and was a perceptive and generous presence at all times.

I have been a student of animal behavior for many years prior to my enrollment in the graduate program at WHOI, therefore, the genesis of many ideas presented in this thesis pre-date my WHOI career. First, I wish to thank those who have been my mentors over the years: Jeanne Altmann and Joan Silk taught me how to study animal behavior, and Karen Pryor gave me a unique perspective on behavior through animal training. Steve Leatherwood and Sam Ridgway provided my first encounters with dolphins at Pt. Mugu, and Ken Norris and Tom Dohl first introduced me to wild dolphins at Kealake'akua Bay. The years I spent observing baboons in Amboseli under the tutelage of Jeanne and Stuart Altmann has had a lasting impact on my thinking about animal behavior. The time I spent observing wild bottlenose dolphins near Sarasota, at the invitation of Randy Wells, Michael Scott, and Blair Irvine, has forever influenced my thinking about the social behavior and social relationships of dolphins.

The Chicago Zoological Society (Brookfield Zoo) has supported me throughout my graduate career in more ways that I can count. I am especially grateful to George Rabb, the director, and Pam Parker, whose joint idea it was for me to return to school for a doctoral degree. As frustrating as the experience has sometimes been, the wisdom of their edict prevailed: this was the right thing for me to do. I thank my collaborator at the zoo, Tara Gifford, for her long-term friendship and support, and I am grateful to the entire Seven Seas staff, past and present, for their assistance and for a unique sense of humor. In particular, I thank Ed Krajniak, Cheryl and Doug Messinger, Marty Sevenich, Tim Sullivan, and Jan Sustman for their special contributions to studying dolphin behavior in a captive setting. I also thank my colleagues in the Conservation

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The National Marine Fisheries Service sponsored the study of Swim-with-dolphin programs. Again, I thank Trevor Spradlin, my collaborator, as well as Aleta Hohn, whose good advice and sense of humor helped us to survive the experience relatively unscathed. Craig Pelton spent long hours observing the dolphins, and Cindy Flaherty spent long hours tabulating data. I also thank Bill Windom, Ann Terbush, and others in the Office of Protected Resources for their support. I am especially grateful to the staffs at Dolphin Quest, Dolphin Research Center, Dolphins Plus, and Theater of the Sea for their hospitality and cooperation during the study.

Dolphins of Shark Bay Research Foundation made it possible for me to conduct field research in Shark Bay, Western Australia. I thank my colleagues, Per Berggren, Richard Connor, Janet Mann, Andrew Richards, and Rachel Smolker, for welcoming me into the project and providing friendship and support. My collaborators, Andrew Richards and Janet Mann, helped me to learn the ropes and the dolphins of Shark Bay. They have been guiding forces in nearly all phases of the project, and along with Rachel Smolker and Kelly Waples, provided long-term data for use in this study. I am also grateful to Richard Connor and Rachel Smolker who initiated the long-term project on

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I thank my parents, to whom this thesis is dedicated, for their encouragement and support long past the recommended cut-off for prudent parental investment. I am grateful to my friends -- Susan Alberts, Jeanne Altmann, Betty Fuller, Pam Parker, Craig Pugh, Carol Saunders, and Kathy Twombly -- for their support and for helping me to see the light at the end of the tunnel. My swimming and running companions, both human and canine, helped me to counteract the stupefying and back-wrecking effects of long hours at the computer.

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With Andrew Richards and Janet Mann

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CHAPTER 1. FLUKEPRINTS:
A HISTORY OF STUDYING THE SOCIAL BEHAVIOR OF CETACEANS

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INTRODUCTION

Cetology is at a turning point with respect to studies of social behavior, a time of transition from qualitative, descriptive natural history to focused, quantitative analyses of the social behavior of whales, dolphins, and porpoises. To set the stage for understanding, appreciating, and advancing this metamorphosis, the present chapter traces the somewhat unconventional route that has delivered us to this pivotal juncture.

Some might insist that writing such a history is a futile effort because there is no entity that can rightfully be labelled "cetacean behavioral biology". Moreover, since there has been negligible direct contact and intellectual exchange with the broader field of animal behavior (whose focus is primarily terrestrial animals), little can be learned of our roots by reviewing the history of animal behavior. In older animal behavior textbooks, cetaceans appear as exemplars of anthropomorphism (the dolphin's smile: Tavolga 1969) or untested sociobiological theory (cooperation: Wilson 1975). Most modern texts, however, are virtually devoid of any new information about cetaceans or their behavior (see, *e.g.*, Hinde 1982; Gould 1982; Dewsbury 1984; Alcock 1993), presumably because studies of cetacean social behavior lag far behind their terrestrial counterparts and have therefore contributed little to contemporary theory and methodology. So, what can possibly be said about the history of a non-field?

It is the nonexistent status of cetacean behavioral biology that cries out for scrutiny. Many whale and dolphin societies are arguably among the most complex in the

mammalian world -- why then has their social behavior been given short shrift? Cetaceans themselves have been subjects of extensive and intensive scientific inquiry -- why then is our knowledge of their social behavior usually a by-product of other non-behavioral investigations? Cetacean sociality and intelligence have engendered enormous popular interest and countless myths -- why then hasn't this favor translated into more scientific inquiry?

The customary answer is that the social behavior of difficult-to-see, difficult-to-follow marine animals is difficult-to-study. There are innumerable, formidable, logistical hurdles that must be surmounted in order to learn about animals whose lives take place primarily beneath the water and whose behavior is typically viewed from unstable platforms at the water's surface. Many cetaceans are fast-moving, wide-ranging, elusive animals, and their behavior is difficult to observe closely at sea. Indeed, studying the social behavior of whales, dolphins, and porpoises in the wild is exceedingly hard work.

Nevertheless, there are numerous non-marine species that are similarly resistant to direct observation because they fly or burrow, are nocturnal or nomadic, live in forest canopies or on ice flows; and yet, many of these animals are subjects of legitimate animal behavior research. A good example is the subterranean naked mole-rat whose social structure and behavior have received considerable scrutiny (*e.g.*, Sherman *et al.* 1991). In addition, primatologists -- whom we customarily think of as striding across the open savannah trailing highly-visible, ground-dwelling monkeys -- have long bemoaned "...the extraordinary obstacles in the way of primate research. In the often remote areas where primates still survive in nature, there are truly formidable difficulties involving logistics, disease, language, culture, and even violence..." (Hamburg 1987: viii). Hardships notwithstanding, field studies of primate social behavior have not only flourished but are an integral part of primatology, featuring not only the terrestrial, accessible baboons and macaques but also such obscure species as the tiny, nocturnal, arboreal galago (*e.g.*, Clark 1978) and the endangered, forest-dwelling muriqui (*e.g.*,

Strier 1990).

For those comfortable in boats, the coastal marine environment can actually be more accessible than many terrestrial habitats. Large concentrations of cetaceans live within close reach of many urban centers and research institutions. The marine habitat, however, is more than merely a hindrance to direct viewing of underwater behavior. The sea is additionally hostile to such tangible signs of lifestyle as tracks, scats, or nests -- a factor with which few land-based biologists have had to contend. Thus, cetacean biologists, handicapped with impaired viewing and imperceptible clues, must be singularly inventive in their efforts to detect and decipher the behavior of whales, dolphins, and porpoises. This chapter is, in part, a celebration of those ingenious methods.

But the difficulty factor alone is not sufficient explanation. This chapter portrays additional, largely historical, factors that have thwarted the progress of studies of cetacean social behavior. Human interests often dictate that certain taxonomic groups, like the cetaceans and the primates, be viewed through special lenses. As a result, cetology and primatology have each come from a very different background, with terminologies, methodologies, and emphases so dissimilar they might as well have come from separate cultures. Thus, this chapter is primarily about the cultural, or historical, factors that are unique to studying cetacean social behavior.

The focus of primate studies was essentially shaped by our desire to know more about the behavior of our hominid ancestors (Washburn and DeVore 1961). In concert with input from evolutionary theory, natural history, comparative psychology, and ethology, the humanistic emphasis in primate behavior and resultant interest in individuality (*e.g.*, Rowell 1994) set a standard for animal behavioral research (*e.g.*, spotted hyaenas: Frank 1986; African elephants: Moss and Poole 1983; northern elephant seals: Cox and Le Boeuf 1977).

In contrast to this anthropocentric fascination with primates, human interest in the cetaceans has had a wholly different derivation. We cared little about cetaceans as individuals because we scarcely considered that the behavior of such strange beings would tell us anything about ourselves. To the contrary, cetaceans are sufficiently alien that they were considered to be appropriate stand-ins for our attempts to prepare for communication with extraterrestrial life (*e.g.*, Wooster *et al.* 1966). Until relatively recently it was debated whether cetacean behavior had any resemblance at all to that of terrestrial mammals (*e.g.*, Darling 1988).

Instead, for centuries, our interest in large cetaceans has been a commercial one. Through the whaling eras of open, human-propelled boats and sailing ships to the modern factory vessels, any knowledge we acquired of the social behavior of the great whales was employed to increase whaling harvests or to manage a lucrative but diminishing resource. As a result of this exploitative association, our understanding of whale social behavior was built upon foundations of population biology, stock management, and analysis of whale carcasses and whaling statistics -- avenues of inquiry whose methods, philosophies, and vocabularies imposed idiosyncratic ways of thinking about and studying whale behavior. As whale numbers and habitats declined, the consumptive attitude shifted to a more conservation-oriented perspective, emphasizing the population and life history parameters of living whales at sea.

Our relationship with small whales, dolphins, and porpoises had a different origin. We hardly noticed the existence of the smaller cetaceans, except as fishermen's pests or mythological beasts, until trained dolphins became the star entertainers of early oceanarium collections. The visibility and accessibility of small cetaceans at aquaria provided close-up viewing and hands-on experimentation opportunities, thus attracting many scientists to investigate the intricacies of cetacean social behavior, sensory systems, and communication. The resultant descriptive studies form the basis of much of what is known today about the social behavior of small cetaceans. Unfortunately, this prolific

period of research was short-lived: anti-captivity sentiments, changes in the character of zoo-based research, and sensationalized reports of human-dolphin communication (resulting in fantastical notions of cetacean sociality and intelligence) have all worked together to discourage further captive research on social behavior.

Throughout, studies of the social behavior of whales and small cetaceans have largely operated in isolation from the broader field of animal behavior. Initially, the few cetologists who studied social behavior found that their interest was not taken up by those investigating the behavior of other taxa. Increasingly, the seclusion of these cetologists left them unschooled in modern methods of behavioral research. Thus, cetology perhaps presents another example of the detrimental effects of "carving up science along phyletic lines... [as] exemplified in studies of non-human primates. Through limiting their vision by phyletic boundaries, primatologists have too often tackled issues with which ornithologists were already highly experienced" (Bateson and Hinde 1976: 529). Although primatologists with behavioral interests have long been integrated into the broader field of animal behavior, the cetologists, by and large, are still estranged.

Today, research on cetacean social behavior is generally one segment of multi-faceted, longitudinal field studies of individually-identified animals. However, because of the difficulty and the cultural factors, cetacean social behavior has rarely been a focus of such projects. Because of cultural factors, in particular, old ways of thinking and out-dated methodologies linger on, and contemporary studies of cetacean social behavior have neither reached their full potential nor caught up to their land-based analogues.

The following narrative outlines how we came to learn what is presently known about cetacean social behavior. Beginning with the hunting tales of the early whaler-naturalists, this account describes the attempts to infer behavior and social structure from studies of whale carcasses; the intimate observations of small cetaceans at early oceanaria; the pseudo-scientific explorations of human-dolphin communication; the

decline of zoo-based research on cetacean social behavior; the evolution of present-day, long-term field studies; and the all-pervasive influence of population biology. As chronicler, I have tried as much as possible to introduce and explain the central events, viewpoints, and concerns in the words of the principal players themselves, a task made all the easier being based on a literature rife with commentary.

As this history unfolds, some good news is revealed for the prospects of cetacean behavioral biology. Despite obstacles imposed by the difficulty and cultural factors, it appears that the groundwork has been laid for sophisticated studies of cetacean social behavior to take place. Long-term research on individually-recognized cetaceans is well-established; extensive demographic, reproductive, and kinship information has been obtained for many individual whales and dolphins; conditions are right for a renewal of the dialogue between captive and field studies; and a theoretical framework and systematic behavioral sampling techniques are available upon request from behavioral biology. With the hard work already accomplished, it is time to usher in focused, quantitative studies of cetacean social behavior.

TRADITIONAL WHALING

The early whaler-naturalists

> *"It is hardly necessary to say, that any person taking up the study of marine mammals, and especially the Cetaceans, enters a difficult field of research, since the opportunities for observing the habits of these animals under favorable conditions are but rare and brief. My own experience has proved that observation for months, and even years, may be required before a single new fact in regard to their habits can be obtained."* Charles Melville Scammon 1874: 11-12

"A long time ago excellent possibilities really existed for observing whales from sailing boats and row boats in immediate proximity. In addition, one should bear in mind that before the invention of the harpoon gun, whalers were forced to study the peculiarities of the whales' behavior in more detail and more scrupulously not only for the success of the whaling but also for their own safety."
Alexey V. Yablokov 1972: 261

Early whalers of the 18th and 19th centuries, like successful hunters of any species, had extensive knowledge about the habits of their quarry. Their targets were the large, slower-moving cetaceans -- such as right, gray, sperm, bowhead, and humpback whales -- that could be approached by human-propelled longboats. Quiet, open-boat whaling techniques brought whalers and their prey into such close quarters that whalemen were able to describe such secretive behavior of sperm whales as nursing (*e.g.*, Bennett 1840; Bullen 1902) and copulation (*e.g.*, Bennett 1840).

Some early whalemen were self-styled naturalists who wrote about whales with intellectual as well as professional interest. The whaling captains, Scammon (1874) and Scoresby (1820), and whaleship surgeons, Beale (1835) and Bennett (1840), published observations of social behavior, school composition, and natural history of large whales. Beale presented scholarly papers on sperm whale behavior to the Eclectic Society of London. Scammon was a contributor to the *Proceedings of the Academy of Natural Sciences of Philadelphia* and *The American Naturalist*, and he published a monumental volume, *The Marine Mammals of the Northwestern Coast of North America*. Of his book, Scammon (1874: 11) said: "The chief object of this work is to give as correct figures of the different species of marine mammals... as could be obtained from a careful study of them from life, and numerous measurements after death, whenever practicable. It is also my aim to give as full an account of the habits of these animals as practicable..." Scammon's book was praised by his contemporaries as one that "only a naturalist who combined his scientific knowledge with the experience of a whaleman" could have written (Allen 1874: 632-3).

"The experience of a whaleman" predisposed whalers to be best informed about those behavioral patterns likely to affect the outcome of the hunt. For example, whalers' knowledge of maternal behavior often condemned mothers and calves as easy targets. Whaleman Nordhoff (1895: 174-5) proclaimed the humpback as "the most stupid of whales [because it] clings obstinately to the [calving] place it has once chosen... The females of these whales... frequent bays and shallow waters yearly, when their time of calving comes on, to drop their young, remaining in the smooth waters until the young leviathan has gained strength enough to shift for himself on the broad ocean. These occasions are taken advantage of by whalemen, and great numbers of the old fish are slain annually in the many unfrequented bays of Africa and South America." Similarly armed with the knowledge that "the right whale mother is very careful to choose a retired and unfrequented roadstead for the scene of her maternal labors" (Nordhoff 1895: 175), whalemen readily preyed upon mothers and calves of that species. Mother sperm whales were known to remain close by "so long as the young showed signs of life. For this reason, whalers, when harpooning calves, tried merely to wound and not kill them, so that both mother and young could be secured" (Caldwell and Caldwell 1966: 759).

Not only did whalers exploit mother-calf bonds, but "the literature of the eighteenth and nineteenth centuries reveals that many whalemen... of that era were aware of the succorant behavior that cetaceans displayed toward their wounded schoolmates, and [used] the knowledge... to increase the whale catch" (Caldwell and Caldwell 1966: 757). Whalers' tales about whales that "hove to" when a schoolmate was distressed or injured (*e.g.*, Beale 1835) formed the basis for present-day hypotheses about "epimeletic" or altruistic behavior of cetaceans (*e.g.*, Caldwell and Caldwell 1966; Connor and Norris 1982). Whalers' recognition of strong bonds between individual whales sometimes enabled them to capture entire social groups of some species. Female sperm whales, in particular, were known to be "remarkable for their strong feeling of sociality and attachment to one another, and this is carried to so great an extent, as that one female of a herd being attacked and wounded, her faithful companions will remain around her

to the last moment or until they are wounded themselves" (Beale 1835: 36).

On occasion, however, whalers' plans went awry when there was "active intervention by sperm whales in the fate of a 'comrade in distress'; for instance, sperms have dived under the ship in order to reach a wounded animal and pull it away from a dangerous spot; in several cases they have broken harpoons, bitten through harpoon lines to free their 'comrade', or even attacked boats and destroyed them..." (Berzin 1972: 256). Open-boat whaling provided excellent opportunities for close-up viewing of, and even direct participation in, the whales' anti-predator responses. Of sperm whales, Beale (1835: 48-9) confirmed that "...these enormous creatures are sometimes known to turn upon their persecutors with unbounded fury, destroying every thing that meets them in their course, sometimes by the powerful blows of their flukes, and sometimes attacking with the jaw and head." California gray whales were considered so dangerous that whalemen regarded them as "a cross between a sea-serpent and an alligator" (Scammon 1874: 272), and the hunt was "appropriately named 'devil-fishing'" (Scammon 1874: 260).

Early whalers were aware of individual whales with distinctive markings and the locations where such whales could be found "even before Melville transformed the true story of an unusually light-coloured Sperm Whale named Mocha Dick into his epic novel, *Moby Dick*..." (Katona and Whitehead 1981: 439). Southwell (1898: 403) reported: "In 1867 [Captain Gray] chased a [balaenid] whale 'with a growth like a beehive on the left side of its tail'; in 1872 he killed this same whale, and almost on the same spot. Writing in 1886, [Captain Gray] said that in 1880 he chased a whale with a large white splash on its back, and that he had seen it every year since. He also states that whalers come to know strongly-marked individuals, and recognize them from time to time, thus showing that the whales follow the same line of migration for many successive seasons."

Southwell (1898: 397-8), however, cautioned against the whalers' inevitable bias: "[I]ntelligent as some of our whalemen have been... it must be borne in mind that their main object is the capture of these valuable prizes, and not for the study of their habits, except in so far as such a knowledge would conduce to that result." And, indeed, early whalers were less familiar with those aspects of social behavior that did not directly influence hunting success. Thus, for example, the belief that the basic social unit of sperm whales consisted of a "schoolmaster" and his "harem" of females (*e.g.*, Bennett 1840) could perhaps be credited more to the whalers' longings in a woman-less society than to their keen powers of observation. Recent evidence refutes the schoolmaster theory, suggesting instead that roving males in search of mating opportunities are short-term visitors to stable matrilineal groups of female sperm whales (*e.g.*, Best 1979; Whitehead and Arnbom 1987; Whitehead and Waters 1990).

Smaller cetaceans -- the dolphins, porpoises and small whales -- were also hunted for food, oil, and skins. "Schools of [long-finned pilot] whales, known in the Faeroes as *grind*, ...are hunted at every opportunity by the Faeroese, among whom the *grind* has a long and venerable history as a source of food. Its importance to the well being of the community has been recognised for over a century by statutes ratifying age-old usage and tradition" (Williamson 1945: 118). "The first record of whales being put to good use in the Faeroes is dated 1584... Doubtless the whaling is of much greater antiquity... and we may safely take it that that year marks merely the beginning of the written records, which thereafter were kept fairly regularly by the Danish Treasury, since a certain income was derived in tithe" (Williamson 1945: 130-1). In Great Britain "...the [common] Porpoise... formed the royal dish even so recently as the time of Henry VIII..." (Norman and Fraser 1937: 310). Later, in the 19th century, a "species of Delphinus [sic], usually called Bottle-nose,... [was] occasionally driven on shore by the inhabitants of Shetland, Orkney, [Faeroe], and Iceland" (Scoresby 1820: 11), and there was "a fishery for the capture of the Bottle-nosed Dolphin ...carried on from Cape Hatteras, North Carolina... [where] between the 15th November 1884 and the middle of

the following May, no less than twelve hundred and sixty-eight of them were caught..." (Norman and Fraser 1937: 328).

Fisheries for the smaller cetaceans tended to be seasonal, land-based operations; therefore, behavioral information from this source was less extensive than that obtained in the course of lengthy voyages in search of large whales. Caldwell and Caldwell (1972: 149) lamented the loss of "tremendous amounts of good data" because serious biological study was rarely a component of the small cetacean fisheries. Nevertheless, turn-of-the-century fishermen had some ideas about the social behavior of their prey (*e.g.*, True 1890). Williamson (1945: 121) found that the Faeroese whalemen recognized and took advantage of the tendency for pilot whales to "behave... very much as though they were a flock of sheep." The whalers also claimed that escaped whales came back to be captured because they "'return to the blood,' as though this exerted some hypnotic influence", an idea that Williamson (1945: 123) rejected, proposing instead that a whale separated from its *flok* [school] was drawn back by strong social bonds. Cape Hatteras fishermen described the behavior of their prey (reported by Townsend 1914: 299), contributing some observations of bottlenose dolphin calves that were only partially correct: "[W]hen very young [the calf] swims just ahead of the mother, and is raised to the surface by her each time she rises to breathe."

Although whalers' accounts were often rendered with a predatory point of view and spiced with stories of "castaways, mutinies, desertions, floggings, women stowaways, drunkenness, ...hostile natives, barratry, brutal skippers..." (Sherman 1965: 22), the wealth of natural history narratives told by whalemen have proven to be a valuable source of behavioral information (*e.g.*, Caldwell *et al.* 1966; Best 1983; Mitchell 1983; Wray and Martin 1983). In many respects, the early whalers' observations and their interpretations of what they saw formed the cornerstone to our understanding of the natural history and social behavior of the large cetaceans.

MODERN WHALING

"Units rather than whales" [1]

> *"Since whaling is a marine enterprise, most patterns of thought that have been devoted to the harvesting of whales have been derived from fisheries biology, where it is customary to think in terms of populations and aggregates rather than individual animals..."* George A. Bartholomew 1974: 295

The modern whaling era "goes back to the invention of the harpoon gun and explosive harpoon head by the Norwegian Svend Foyn in the 1860s; but it was the development of the floating factory in 1903, and especially of the factory ship stern ramp in 1925... which made expansion into all Antarctic seas possible" (McHugh 1974: 321). Technological advances enabled whalers to hunt such fleeter species as blue, fin, sei, Bryde's, and minke whales, as well as the sperm whales that had been accessible to early whalers. However, "the rapid and more intensive catching methods using noisy, propeller-driven catchers gave less time and opportunity for observations of undisturbed behavior... For a long time after the end of open-boat whaling, therefore, first-hand observations and new data on social behavior... were slow in coming" (Best 1979: 228). As an example, Best (1979: 251-4) noted that "although eyewitness accounts of battles between individual sperm whales exist in the literature of open-boat whaling (see Caldwell *et al.*, 1966), only one modern account of such behavior exists (Zenkovich, 1962). This may be because the presence of screw-driven vessels can be detected by sperm whales at a distance of up to eight miles, when their behavior usually changes markedly (Gambell, 1968)."

Crews of spotter aircraft sometimes came upon rare spectacles, such as the calving behavior of sperm whales (Gambell *et al.* 1973) or the protective behavior of humpbacks towards calves during a killer whale attack (Chittleborough 1953). Scientists

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[1] McVay 1974: 374

on whale-catching and marking expeditions also recorded behavioral events (*e.g.*, fin and humpback whales: Andrews 1909; fin whales: Gunther 1949; sperm whales: Berzin 1972; gray whales: Bogoslovskaya *et al.* 1982); and True (1903), aboard a catcher, produced some of the first photographs of living whales at sea. As in the open-boat era, it was the whales' defense against their human predators that was most commonly seen from the whalers' vantage point. A well-known example is "a very strange habit" of sperm whales described by Nishiwaki (1962: 2): "A group of sperm whales, about 20-30 individuals swimming leisurely, was found. The whale catcher approached very slowly and then shot the biggest whale. The instant the whale was hit all individuals of the herd made a circle like a marguerite flower [daisy] centering around the biggest whale. These radially gathered whales put their heads together and made many splashes with their tail flukes."

Although mechanized techniques reduced opportunities for first-hand observation, modern whaling did provide an incentive to better understand the social behavior and social structure of whales because "effective management of heavily exploited wild species obviously requires that harvesting procedures be based on accurate knowledge of their natural history" (Bartholomew 1974: 294; and many others, *e.g.*, Schevill 1974, Winn and Olla 1979). With establishment of the International Whaling Commission (IWC) in 1946, regulatory decisions were mandated to be based on scientific findings (McHugh 1974). Unfortunately, despite "the large body of scientific data about the biology of whales, almost the only aspect of this knowledge that has been used by the whaling industry is information on the abundance of whales and where they can be found" (Bartholomew 1974: 294). The mandate was further undermined because equal consideration was accorded to non-scientific factors (McHugh 1974), which meant that IWC decisions also weighed the financial concerns of the whaling industry and the preservationist attitudes of environmentalists (Peterson 1992). An egregious example of the controlling influence of economics in whaling management was the "blue whale unit", defined as "an arbitrary expression intended to equate different whales on the basis of the

amount of oil produced from them. In its later form 1 blue whale was considered equivalent to 2 fin whales, or to 2.5 humpbacks, or to 6 sei whales. This, while convenient for the whalers, was an unfortunate idea for conservation" (Schevill 1974: 414).

Scientific input did prevail in IWC decisions during the 1970s. As a first step, Bartholomew (1974: 295) urged cetologists to "use as our point of departure not fishery biology, but the ecology and social behavior of the large mammals -- which, to say the least, is what whales are..." With establishment of the New Management Procedures, "the Scientific Committee [was made] far more important... [by raising] the level of scientific argumentation that went into decision making. Before 1974, the members of the Scientific Committee had given the IWC a unanimous 'best estimate' resting as often on political as scientific grounds... Spurred by pressures from outside cetologists and from members of the IUCN and the FAO... the Scientific Committee used the adoption of the new management procedures to establish a more open process in which papers were published, commentary was sought, and the scientific basis of conclusions was made explicit" (Peterson 1992: 164-6). As a result, "the Twenty-fourth Meeting of the Commission [in 1972] was notable in a number of respects [including seeing] the end of the blue whale unit as a method of regulating catches..." (IWC 1974: 6) and its replacement with biologically-relevant quotas related to species and breeding populations.

Such changes paved the way for regulatory decisions based on more refined understanding of behavior, including the idea that sperm whale "social structure is such that the simpler population models are not at all applicable" Holt (1977: 133). Many agreed that "both the underlying biology and the manner of harvesting demand that any management model for sperm whales should distinguish between the sexes" (Beddington and Kirkwood 1980: 57). Thus, even though male mammals are seldom considered in demographic models, specific attention was given to adult male sperm whales and "separate [catch] limits for male and female whales in this species were set" (IWC 1974:

6). Considerable effort ensued to determine which social and demographic factors were critical to developing accurate models (*e.g.*, IWC 1980). For example, after reviewing the survivorship of long-lived mammalian species, Ralls *et al.* (1977: 241) rejected "the current assumption of equal mortality rates for males and females in [sperm whales]... on both theoretical and comparative grounds." In addition, the reproductive role of male sperm whales was a particular concern, stemming from the early whalers' belief that males were "harem masters". Cetologists like Mitchell (1977: 224) worried that selective whaling for large males would have disastrous effects:

> "Behavioural processes occurring during the rendezvous between bulls and schools of mature females are unknown, as is the possibility of replacement of breeding bulls during the mating season. It is not certain whether the 'idle' bulls take turns at being harem master... or whether bulls, once they reach this 'idle' status and assume lengthy, high-latitude migrations, are ever again candidates for 'harem master' status... If behavioural and distributional factors insured that after competition for harems, the successful harem master would be the only male servicing a harem... then the removal of the harem master could reduce pregnancy rates in that school drastically..."

In light of current knowledge that males move between groups of females (*e.g.*, Best 1979; Whitehead and Arnbom 1987; Whitehead and Waters 1990), this concern now seems less urgent (Whitehead 1990).

Despite these concessions to male sperm whales, the overall impact of behavioral considerations on whaling management was minor. In contrast, the strong management emphasis in cetology did exert substantial influence on how scientists thought about and conducted research on whale behavior. Perceptions of whale behavior were all-the-more clouded because whaling science embraced and perpetuated 'group selection', a popular social theory that disputed Darwinian natural selection at the level of the individual. Outspoken proponent of group selection, Wynne-Edwards (1962: 14), named social displays as the vehicles by which animals assessed their population density, concluding that "social organisation is originally set up... to provide feedback for the homeostatic machine." Wynne-Edwards (1962: 18-9) cited circumstances in which:

> "...the interests of the individual are actually submerged or subordinated to those of the community as a whole. [For example] the social hierarchy... is a common and important product of conventional competition, and its function is to differentiate automatically, whenever such a situation arises, between the haves and have-nots... For those high enough in the scale the rewards -- space, food, mates -- are forthcoming; but when food, for instance, is already being exploited up to the optimum level, the surplus individuals must abide by the conventional code and not remain to contest the issue if necessary to the death. It is in the interests of survival of the stock and the species that this should be so, but it ruthlessly suppresses the temporary interests of the rejected individual, who may be condemned to starve while food still abounds."

In particular, "what Wynne-Edwards proposed was the specific hypothesis that animals voluntarily sacrifice personal survival and fertility to help control population growth... [and] that this is a very widespread phenomena among all kinds of animals" (Wilson 1975: 110).

For a time, species-benefit reasoning influenced thinking about the social behavior of all animals, and many "early ethologists often assumed that natural selection would produce animals that sacrificed personal reproductive success for the general benefit of their species..." (Alcock 1993: 10). Cetologists such as Caldwell and Caldwell (1972: 57-8), like their counterparts studying terrestrial animals, used this rationale to explain behavioral phenomena: "The subadult male [dolphin] is biologically expendable to the herd, being lower in the social hierarchy than the herd bull and less likely to impregnate the females. Thus by acting as scouts [in times of danger], the subadult males help protect the herd without endangering its longterm social structure or reproductive potential, and thus help maintain the species."

The group-focused standpoint was ultimately shown to be largely erroneous when applied to the evolution of social behavior. "Wynne-Edwards' advocacy of group selection... had the ...effect of stimulating a careful examination of the issues involved, leading to the conclusion that group selection is unlikely to be of widespread importance" (Gadgil 1982: 490; and many others). As a result, Darwinian natural selection with its

focus on the individual soon regained prominence in evolutionary biology and animal behavior (*e.g.*, Lack 1966; Williams 1966; Wilson 1975). With this conceptual shift, traditional explanations were reframed at the level of the individual, resulting in more comprehensive interpretations of behavioral phenomena. Hrdy (1977) gave this example: infanticide by male langur monkeys was historically explained as a means of regulating population numbers in the face of over-crowding; infanticide was now better understood as a reproductive strategy of individual males of a number of species, including lions, colobus monkeys, ground squirrels. Many apparently altruistic acts, previously assumed to be sacrifices for the good of the group, were now better understood as aid to close relatives (Hamilton 1964).

Group selection explanations had considerable impact on cetology because explicit links were made to whaling management. In developing his ideas, Wynne-Edwards (1962: 7-8), "took as his starting point an analogy from the whaling and fishing industry. Noting that 'overfishing reduces both the yield per unit effort and the total yield', he argued that animals are no different in principle from fishermen. They must manage their own number to prevent overkilling their own prey" (Le Boeuf and Würsig 1985: 134). The same views were then produced as endorsement for whaling practices in that the "notion of self-regulation of animal numbers by 'self-destruction' for the good of the group was in accord with management philosophy... and justified culling. Culling saved animals the trouble of having to do it themselves" (Le Boeuf and Würsig 1985: 134-5). Whaling managers were loath to part with these ideas because, after all, group selection was an appropriate point of view for how humans should manage an animal resource to maximize yield from a population.

The favor these ideas found in whaling management inevitably spilled over into how cetacean biologists talked and thought about whale behavior. In particular, whaling terminology, coined to facilitate resource management, effectively discouraged thinking about whales in ways that were biologically significant. Not only was the blue whale

unit "an unfortunate idea for conservation", but as McVay (1974: 374) pointed out, "by talking in 'units' rather than 'whales,' you make it arithmetic, not biology". Talking in terms of blue whale units, stocks, and barrels was not conducive to thinking in terms of species, breeding populations, or individual whales. To promote a change in focus, Bartholomew (1974: 295) urged fellow cetologists: "Perhaps instead of thinking of whales in terms of aggregates, we should think about them as individuals operating in a social context that is maintained by complex individual social interactions." A decade later, Le Boeuf and Würsig (1985) re-emphasized the importance of this conceptual shift to the increasing sophistication of cetacean behavioral research.

Today, most scientists concede that group selection models generally "apply to extremely specialized conditions and provide no explanation for the evolution of altruistic traits in vertebrates, except in groups of related individuals" (Clutton-Brock and Harvey 1978: 6; see also Maynard Smith 1976). Kin-based colonies of social insects that form "complex cooperative societies with such internal cohesion and division of labor that they resemble single organisms" (Trivers 1985: 171) still evoke a group-focused perspective (*e.g.*, D. Gordon 1987). Hölldobler and Wilson (1994: 107) maintain that: "One ant alone... is really no ant at all... The amazing feats of the weaver ants and other highly evolved species comes not from complex actions of separate colony members but from the concerted actions of many nestmates working together... The colony is the equivalent of the organism, the unit that must be examined in order to understand the biology of the colonial species." Thus, "to speak of a colony of driver ants or other social insects as more than just a tight aggregation of individuals is to speak of a superorganism, and therefore to invite a detailed comparison between the society and a conventional organism" (Hölldobler and Wilson 1994: 110).

Group-level ideas also play a role in contemporary interpretation of the behavior of some cetaceans. Jerison (1986: 163-4) noted that "information from echolocation can be sensed at the same time by several individuals", which led him to suggest that

dolphins may experience "communal cognition", something akin to "an extended self... constructed (and experienced) by a group of several animals..." In addition, Norris's (1991*c*: 13) long-term study of Hawaiian spinner dolphins led him conclude that, as with colonial ants, "a spinner dolphin alone is very much less than a whole animal." Norris (1991*c*: 13-4) elaborated: "It was only after much looking that we began to understand another key feature of [the spinner dolphins'] lives: they are so thoroughly creatures of their schools that they have surrendered some aspects of normal mammalian individuality to the group... [Spinner dolphins] live locked in the geometry of their schools, playing out a life-long cat-and-mouse game with their predators... [The dolphins'] ultimate defense is to behave like schooling fish. In doing so, their individuality is suppressed in favor of the school." At other times, with echolocation providing an early warning system to detect predators, dolphins can "afford to express all the complexity and individuality of their mammalian heritage... But should the predator swim close, they then must revert to the fish's strategy, the school, in which they become faceless ciphers, obeying without question a group strategy" (Norris 1991*c*: 180-1). Is this something more than Hamilton's (1971) "selfish herd"? Well-known for provocative ideas that have inspired the careers of innumerable cetacean biologists, Norris's intriguing but controversial proposal awaits its turn for further scientific scrutiny.

Shoot first, ask questions later: Deductions about behavior from dead animals

> *"There is no firm evidence that the post-reproductive phase occupies a major portion of the total life span of the females of any wild mammal other than* ***Globicephala macrorhynchus****... One of the best ways to obtain this information is to use the carcass-salvage approach on a large sample of conspecifics obtained through a fishery..."* Helene Marsh and Toshio Kasuya 1984: 334

A major contribution of modern whaling to understanding behavior comes from a paradoxical source: much of what we know about social behavior and social structure of large cetaceans has been inferred from dead bodies. Making deductions about social

structure and behavior based on studies of cadavers was not unique to cetacean research. Zoology had a long tradition of emphasis on "comparative anatomy and the study of corpses rather than the behavior of living organisms" (Dewsbury 1973: 8). Investigations of hominid evolution in physical anthropology came from an anatomical perspective: measurement of monkey and ape parts preceded a shift to studies of living primates (Washburn 1951). Carcass analyses were also a component of research on African elephants, conducted in the course of culls intended to preserve woodland habitat (*e.g.*, Douglas-Hamilton and Douglas-Hamilton 1975). Elephant carcass studies, however, were directly descendent from the cetacean research, having been conducted by cetologist, Richard Laws, who modelled his methods for estimating age, maturational status, and reproductive condition of elephants (*e.g.*, Laws and Parker 1968) on his whale carcass studies (*e.g.*, Laws 1956).

Making deductions about the behavior of difficult-to-see animals based on physical remains resembles the work of paleontologists who make inferences about behavior and social structure of never-seen, extinct animals based on fossils. By examining fossilized bones, tracks, and assemblage compositions, paleo-ethologists attempt to reconstruct the lives of such dinosaurs as carnivorous *Deinonychus* that probably hunted in packs (Ostrom 1986) and duck-bill *Maiasaura* that may have provided care for its young in colonial nests (*e.g.*, Horner and Makela 1979; Horner 1982). However, whereas paleo-ethologists are usually limited to small pieces of a few specimens, cetacean carcass analyses have been based on an enormous sample of bodies and even intact social groups.

A staggering number of whale carcasses was available for study: during 1957-1961, for example, Mackintosh (1965) estimated the average annual world catch to be 64,308 whales including 31,326 fin whales, 21,155 sperm whales, and 3,598 humpbacks. By processing entire bodies and analyzing whaling statistics, cetologists were able to conduct truly cross-sectional life history studies (*e.g.*, humpbacks: Chittleborough 1954, 1955*ab*, 1958, 1959, 1960, 1965; sperm whales: Best 1967, 1968, 1969*ab*, 1970; Best

et al. 1984).

Such a solid foundation of life history data provided a basis from which cetacean behavior, social structure, and mating systems could be deduced. For example, a leading theory about cetacean learning arose from carcass analyses. Brodie (1969: 312) observed that "the most striking difference between odontocete and mysticete reproductive cycles is the significantly longer nursing period of odontocetes... [which] is attributed to more sophisticated navigational training, kin-cooperation and complex social structure." Colleagues have praised Brodie as "one of the first to suggest that the prolonged period of lactation in odontocetes may be related to the importance of social learning" (Tyack 1986*a*: 145).

As another example, careful studies of cyamid infestations on whale carcasses enabled further decoding of the complex social structure of sperm whales in the southern hemisphere:

> "The infestation of ...male and female sperm whales involved only two species, *Neocyamus physeteris* and *Cyamus catodontis*... Females and small males both appear to be infested almost exclusively with *N. physeteris*, but ...by a body length of 42 feet males are infested exclusively with *C. catodontis*. The point at which 50 per cent of males are infested with either cyamid species is at a length of 39 to 40 feet, and this stage must correspond to one at which male sperm whales become segregated from female schools... [I]t would seem reasonable to assume that at this stage male sperm whales on average enter the Antarctic for the first time. Thus a significant change in the behaviour of the male occurs at the size corresponding to the attainment of puberty..." (Best 1969*a*: 12).

Carcass analyses, combined with behavioral observations, were also used to evaluate mating strategies of male baleen whales. Brownell and Ralls (1986: 107) found that "the exceedingly large testes of the right whale, its longer penis and the apparently much less aggressive interactions between males in mating groups suggest that this species has been selected primarily for competition through multiple matings and sperm competition", whereas contrasting characters of humpbacks indicated that "males of this

species compete primarily by attempting to prevent mating by other males."

Carcass studies provided heretofore unobtainable information about small cetaceans as well. Drive-fisheries capturing entire social groups have been an important source of information about the social organization of small whales and dolphins. For example, by assessing age, sex, body length, and reproductive status of short-finned pilot whales captured in Japanese fisheries, Kasuya and Marsh (1984: 307-8) attempted to reconstruct the social structure of the species: "[T]he *Globicephala macrorhynchus* school is usually a breeding unit composed of adult males, adult females of various reproductive stages..., and immature and pubertal individuals of both sexes... Females probably attain sexual maturity in their mother's school. The association of females persists for a long time... presumably for life..." Based on genetic data obtained in Faeroese fisheries for closely-related long-finned pilot whales, Amos *et al.* (1991) confirmed the matrilineal nature of social groups but disputed the Kasuya and Marsh (1984) notion that males are long-term members of female groups. "Upon reaching maturity, males probably leave their natal pod and begin to visit other pods, mating with receptive females they encounter... [Adult males] tend not to be associated with any one pod themselves for any great length of time" (Amos *et al.* 1991: 267).

From carcass analyses, Marsh and Kasuya (1984, 1986) also concluded that postreproductive females appear to be an integral part of pilot whale society, an exciting discovery for behavioral biologists and anthropologists alike. The rarity of this phenomenon among mammals has engendered considerable discussion about the possible role of elderly females as caretakers of grand-offspring or as repositories of knowledge (*e.g.*, macaque and langur monkeys: Hrdy 1981; vervet monkeys: Fairbanks and McGuire 1986; Fairbanks 1988; cetaceans: Marsh and Kasuya 1991; Norris and Pryor 1991). Austad (1994: 258) affirmed the importance of the cetacean example: "[T]he single convincing example of substantial female postreproductive life in nature is the short-finned pilot whale... In this species, [Kasuya and Marsh (1984) found] that

reproduction had ceased by the age of forty, that 24% of mature females were postreproductive, and that life expectancy at complete reproductive cessation was still approximately 14 years. The potential parallel with the parental care strategy of humans seems clear."

There are drawbacks to making inferences about longitudinal behavioral processes from a cross-sectional carcass perspective, and consequently, attempts to infer behavior from dead bodies have not always been successful. For example, the oft-cited notion that "baleen whales are generally believed to tend towards a monogamous mating system" (Lockyer 1984: 28) likely originated with Nemoto's (1964) analysis of catch statistics for baleen whales on the feeding grounds. Mackintosh (1965: 38) summarized the report: "From Nemoto's material it seems that schools of baleen whales contain an almost random mixture of whales of different sexes, ages, and sexual condition, though there might be a tendency for males and females to form pairs before departing for the breeding grounds." Recent studies of living animals indicate that monogamy is an unlikely mating system for most baleen whale species (reviewed in Tyack 1986*a*).

Whereas paleo-ethologists will never have the luxury of confirming their theories about dinosaur sociality from first-hand observation, cetacean biologists have been developing ingenious ways to directly and indirectly monitor the behavior of their elusive subjects. Research on living cetaceans, discussed below, will be the ultimate test of ideas about cetacean social behavior that have been generated by carcass analyses.

STUDIES IN CAPTIVE SETTINGS

Marine Studios: "A window in the sea" [2]

"Less than 50 years ago virtually nothing was known about the social...

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[2] Hill 1956

behaviors of dolphins. Their underwater activities were effectively hidden from view, and since scientists had little comprehension of the behavioral attributes of these small toothed whales, there was neither incentive nor guidance for undertaking field studies... This situation changed rapidly when the first oceanarium, Marine Studios..., opened in 1938. Here, for the first time, scientists, along with the public could observe bottlenose dolphins at close range and for extended periods from below as well as above the surface." Forrest G. Wood 1986: 331

"Aquariums can take credit for first bringing dolphins and whales to the world's attention as remarkable mammals that have family life and social behaviour analogous to other mammals. Before this these animals were seen merely as sources of meat, oil and leather products." Murray A. Newman 1994: 212

Because small cetaceans were commercially less important than large whales, little was known about their behavior and natural history until studies were conducted in captive settings. Earliest records of public cetacean exhibitions date back to the 1860-70s when beluga whales, bottlenose dolphins, and a harbor porpoise were exhibited in aquaria in Great Britain and the United States (Wood 1973; Defran and Pryor 1980). A beluga displayed in New York City in the 1860s by celebrated circusman P.T. Barnum was probably the first cetacean trained to perform for the public (Caldwell and Caldwell 1972; Wood 1973). In the early 1900s, aquarium director Townsend (1914: 289) boasted that "New York Aquarium has a school of porpoises and lays claim to the world's best single exhibit of captive wild animals." Fascinated by "the naturally sociable and gregarious habit of porpoises", Townsend (1914: 291-2) provided the first scientific report on the behavior of captive dolphins including a preliminary description of a "wuzzle" [3]: "Frequently three or four [dolphins] will bunch together in the center of the pool, rolling and rubbing against each other in a ball-like mass suggestive of the tussling of puppies." By the early 20th century, small cetaceans were viewed in aquaria throughout Western Europe and the United States (Defran and Pryor 1980). In these early collections, however, it was the rare animal that lived long and none produced

[3] Coined by W. E. Schevill (quoted in Johnson and Norris 1994: 250)

surviving offspring; thus, the scope of behavioral research was limited.

Establishment of Marine Studios in 1938 marked the beginning of a new era in the public display of small cetaceans. Long-time director of Vancouver Aquarium, Newman (1994: 81-2), recalled:

> "The first successful cetacean exhibition was created not by aquarists but by the film industry. In the 1930s a group of movie producers constructed a large tank just outside of St. Augustine, Florida, filled it with marine life and named it Marine Studios. Their objective was to use it as a safe, convenient set for undersea adventure movies. However, the place excited so much local interest that they soon realized more money could be made by charging admission to their exhibit. In a quick change of strategy, they renamed the huge tank Marineland of Florida and presented the world with its first oceanarium. Marineland's undisputed stars in those days were a colony of bottlenose dolphins... maintained and observed by curator Arthur McBride and his successor, F. G. Wood."

"[W]hen the concept of oceanariums was new, no one realized what remarkable creatures [dolphins] were. To Arthur McBride, the first curator at Marine Studios, they were just another possibility for a passive exhibit" (Norris 1974: 56). However, McBride (1940: 16) quickly realized he had something more than a static display, and he was soon "introducing the readers of *Natural History* to one of their most 'human' deep-sea relatives... an appealing and playful water mammal who remembers his friends and shows a strong propensity to jealousy and grief."

The unique underwater viewing opportunities and the stories of sociable dolphins attracted many behavioral scientists to Marine Studios, including up-and-coming comparative psychologist, D. O. Hebb, from the nearby Yerkes Laboratories of Primate Biology, who collaborated with McBride in a pioneering study of bottlenose dolphin social behavior (McBride and Hebb 1948). Other studies of the social behavior of small cetaceans soon followed, at Marine Studios (*e.g.*, McBride and Kritzler 1951; Wood 1953; Tavolga and Essapian 1957; Essapian 1962, 1963; Tavolga 1966), and at captive facilities world-wide (*e.g.*, California: Norris and Prescott 1961; Caldwell and Caldwell

1967; Hawaii: Bateson 1974; the former Soviet Union: Bel'kovich *et al.* 1970; Denmark: Andersen and Dziedzic 1964; and South Africa: Tayler and Saayman 1972).

Interest in cetacean social behavior was further enhanced by improved survival and breeding success at early oceanaria (*e.g.*, Wood 1977; Prescott 1977). The first of a succession of live captive births was recorded at Marine Studios in 1947, and the mother, a bottlenose dolphin named Spray, lived to produce five calves of her own (Wood 1973, 1977). Captive colonies containing a diversity of life stages provided opportunities for studying many aspects of cetacean social life. Caldwell and Caldwell (1972: 31) noted: "Only in oceanariums with communities of captive dolphins can... scientists ...regularly and conveniently observe a semi-natural colony of these aquatic mammals as they play, fight, form deep bonds of affection, reproduce, rear their young, and perhaps even die of old age..."

These early natural history accounts furnished the first-ever -- and in some cases, the only -- glimpses into certain aspects of dolphin social life. Not all observations from early oceanaria have endured subsequent scrutiny. For example, on the basis of their observations of wild dolphins, Wells *et al.* (1980: 303) rejected the McBride and Kritzler (1951) idea "that the basic social unit for Atlantic bottlenosed dolphins was a family unit consisting of a single adult male and three to five adult females with either first- or second-year offspring." Instead, Wells *et al.* (1980) found that the composition of wild bottlenose dolphin groups was fluid, with notable long-term associations among adult males or between mothers and their young.

A few other examples, however, illustrate the extent to which these initial descriptions have contributed to our current understanding of social relations of small cetaceans. The Caldwells were among the first to recognize that "individual recognition and attachment... play a major role in cetacean behavior" (Caldwell *et al.* 1963: 9), and they emphasized the importance of "strong bonds of affection between individuals in

captivity... Not only do two animals prefer to associate more with each other than with others in the same captive colony, but these relationships are often retained for long periods of time even when the animals are separated" (Caldwell and Caldwell 1972: 54). Pre-dating present awareness of long-term bonds that exist between certain male bottlenose dolphins in the wild (Wells *et al.* 1987; Connor *et al.* 1992), McBride (1940: 25-6) described a close relationship of two adult males at Marine Studios: "Because the two males were captured together, apparently their social relationship had been determined previously... There was practically no fighting between the two, and aside from occasional jaw-snapping on the part of the larger, the two were very peaceable... When the [smaller] animal was released into the tank [after a several-week separation], the greatest amount of excitement on the part of the larger male was exhibited. No doubt could exist that the two recognized each other... For several days, the two males were inseparable."

Captive research also led to a refinement of whalers' perceptions of cetacean care-giving behavior. New information about the succorant behavior of small cetaceans was obtained, not only during captures for aquaria (*e.g.*, Brown and Norris 1956; Siebenaler and Caldwell 1956; Norris and Prescott 1961), but also from detailed observations afforded by captive settings (*e.g.*, McBride 1940; Brown and Norris 1956; Tavolga and Essapian 1957; Norris and Prescott 1961; Lilly 1963*b*; Caldwell *et al.* 1963; Caldwell and Caldwell 1966). Care-giving behaviors such as supporting-another and standing-by could be closely examined and sometimes better understood within the context of known relationships of participants. Caldwell and Caldwell (1964) even carried out experimental studies that led them to conclude that supporting behavior was a social response, not merely an action elicited by floating objects (as suggested by Slijper (1962)), based on dolphins' differential reactions to "inanimate" (a log) *vs.* "animate" (a "life-like" vinyl calf and a thawed carcass!) stimuli. A subsequent review of care-giving behavior both in captivity and the wild (Caldwell and Caldwell 1966) resulted in some general conclusions about cooperative behavior of odontocetes: "[I]t appears that usually

only young of either sex or adult females are aided. Adult males do not commonly receive help... It is also much more likely that support will be given to an animal familiar to the group than a stranger -- even if the criteria for proper age and sex are met" (Caldwell and Caldwell 1972: 59). This assessment is now better understood in light of recent indications that many odontocete groups have a matrilineal basis (*e.g.*, bottlenose dolphins: Scott *et al.* 1990*a*; killer whales: Bigg *et al.* 1990).

Contemporary summaries of bottlenose dolphin agonistic behavior (*e.g.*, Shane *et al.* 1986) are still largely derived from reports that are decades old (*e.g.*, McBride 1940; Tavolga 1966). Despite the qualitative nature of those early studies, some findings have, in fact, been confirmed by recent quantitative analyses (Samuels and Gifford, in press). For instance, there was general agreement that adult males were dominant to adult females (*e.g.*, Tavolga 1966; Tayler and Saayman 1972; Samuels and Gifford, in press), and that the agonistic dominance of adult males was distinct from the role of certain adult females as the social foci of their groups (Tavolga 1966; Samuels and Gifford, in press). In early studies, however, dominance relations among adult females were typically dismissed as inconsistent or nonexistent (McBride and Hebb 1948; Tavolga 1966); whereas recent quantitative analysis suggests that, although agonism among females is rare, females may have stable dominance relationships (Samuels and Gifford, in press).

Accomplishments of the early oceanaria have had long-lasting effects. An important, early discovery was that small cetaceans could be readily trained to perform complex behaviors. Caldwell and Caldwell (1972: 14) remembered that:

> "Dolphins had been jumping for food and doing simple... tricks at Marineland [of Florida] for some time, but one night Cecil M. Walker, Jr. (then a night pumpman and now assistant general manager), happened to notice that one of the bottlenosed dolphins seemed to be tossing a pelican feather toward him. Walker retrieved it and with patient coaxing developed this behavior pattern until the dolphin was tossing not only the feather but also such substantial objects as pebbles, rubber balls, and small inflated rubber inner tubes... Step by step this

> simple game developed into the highly trained dolphin shows that can be found in widely scattered corners of the world today."

Soon, Marineland was proudly exhibiting Flippy, the world's first "educated porpoise", tutored by Barnum and Bailey circusman Adolf Frohn (Hill 1956: 181).

It was not only the public that benefited from the cetacean responsiveness to training. "[P]ublic oceanariums have focused ...scientific attention upon the remarkable attributes of the smaller odontocete cetaceans, such as bottlenose porpoises and pilot whales. As a corollary to this new interest, the biologist now finds that he can deal directly with a porpoise as an experimental subject..." (Norris 1966: v). This led to productive areas of research on cetacean sensory systems, communication, and cognition, initiated in the United States during the 1950-60s (*e.g.*, Lilly and Miller 1961*b*; Lilly 1965; Bastian 1967) and in the former Soviet Union by the 1970s (reviewed in Linegaugh 1976).

Norris (1991*b*: 295) recalled that "the first conditioned response experiment on a dolphin" was conducted by Lawrence and Schevill (1954), in which they demonstrated that a bottlenose dolphin could hear sounds above the hearing threshold of humans. In a subsequent experiment, Schevill and Lawrence (1956: 13) showed that a dolphin could find food in water so murky that sight was precluded, "thus supporting the widespread supposition (for example, Kellog, Kohler and Morris 1953) that... cetaceans hunted [by means of echolocation]." Norris *et al.* (1961) went on to train a bottlenose dolphin to find underwater targets while blindfolded, providing more evidence for an ability to navigate using echolocation.

In the "creative porpoise" experiment, Pryor *et al.* (1969) trained two rough-toothed dolphins to spontaneously display novel behavior. Pryor (1975: 236) described the initial trials with the dolphin Malia: "She thought of things to do spontaneously that we could never have imagined, and that we would have found very difficult to arrive at

by shaping... Malia seemed to have learned the criterion: 'Only things which have not been previously reinforced are reinforceable.' She was deliberately coming up with something new..."

Highly-trained dolphins enticed the U.S. Navy to become a principal player in captive cetacean research. "Notty, the Navy's first porpoise" was acquired in the 1960s as part of an effort to improve the hydrodynamics of torpedoes (Wood 1973: 185). Soon thereafter, the Navy embarked on the man-under-the-sea program after losing to the Air Force a bid to supply life-support systems for the man-in-space program (Wood 1973). Motivation notwithstanding, some Navy scientists "thought the exploration of the ocean was just as important as venturing into space, and they had begun plans to study dolphins. They wanted to know how dolphins could swim so fast and silently beneath the ocean's surface, how their sonar worked, how deep they could dive... [reasoning that] the answers to those questions might be useful to humans trying to live and work under the sea" (Ridgway 1987: 10).

Although largely uninterested in cetacean social behavior *per se*, the Office of Naval Research (ONR) sponsored the earliest symposia on cetacean research in 1963. Published proceedings from those meetings (Tavolga 1964; Norris 1966) have been key references for those interested in cetacean social behavior, cognition, and communication. ONR also played a major role in promoting early captive research on sensory systems, sponsoring, for example, nearly all of the studies on echolocation, communication, and cognition listed above (*e.g.*, Lawrence and Schevill 1954; Norris *et al.* 1961; Bastian 1967; Pryor *et al.* 1969). ONR was also a sponsor of the early work of John Lilly (*e.g.*, Lilly and Miller 1961*ab*). However, it was Lilly's later work and ideas, described below, that had widespread influence on studies of cetacean social behavior.

"The Mind of the Dolphin" [4]

> *"...I invite you to entertain some new beliefs about dolphins ...[that] these Cetacea with huge brains are more intelligent than any man or woman."* John C. Lilly 1978: 1 [emphasis is Lilly's]

> *"Individual dolphins and whales are to be given the legal rights of human individuals... Research into communication with cetaceans is no longer simply a scientific pursuit... We must learn their needs, their ethics, their philosophy, to find out who we are on this planet, in this galaxy. The extraterrestrials are here -- in the sea."* John C. Lilly 1976: 68

Since the early captive studies, the notion of a "mind in the waters" (McIntyre 1974) has pervaded research on cetacean social behavior. The individual who popularized this concept was John Lilly, a medical doctor with expertise in neurophysiology. Like many scientists of the day, Lilly gained entry to cetology *via* Marine Studios in Florida. Former curator Wood (1973: 3) remembered that: "Dr. Lilly had first visited the laboratory in 1955 as a member of what we called the 'Johns Hopkins Expedition' ...[a group of] distinguished neurophysiologists... [T]heir purpoise [sic] in coming to Marineland was to map the cortex of the bottlenose dolphin... But they did not foresee the difficulty they would encounter in anesthetizing a porpoise..." After much trial-and-error, Lilly (1958, 1961*a*) worked out methods to study brain functioning using less-problematic local anesthetic and electrical stimulation.

His brain research led Lilly to champion the theory that "the absolute size of the mammalian brain determines its computing capability...; the larger the computer, the greater its power" (Lilly 1967*a*: 33; see also Lilly 1963*a*), thus rekindling a turn-of-the-century debate about the link between brain size and intelligence (*e.g.*, Gould 1981; Jerison 1986), a controversy still raging today (*e.g.*, Klinowska 1988). Brain research, however, also caused Lilly to "become a special target of antivivisectionists..." (Wood 1973: 13).

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[4] Lilly 1967*a*.

While at Marine Studios, Lilly (1961*a*) listened to Wood's (1953) recordings of dolphin sounds and became fascinated by the then-unfamiliar calls made by his dolphin subjects. Lilly provided some of the first structural descriptions of dolphin vocalizations (*e.g.*, Lilly and Miller 1961*ab*; Lilly 1963*b*), many of which are still considered valid today (*e.g.*, Caldwell *et al.* 1990). He also called attention to the dolphins' facility in imitating sounds (Lilly 1961*a*, 1965), leading to studies of vocal mimicry, an important area of contemporary cetacean research (*e.g.*, Richards 1986; Tyack 1986*b*; Janik and Slater, in press). However, Lilly's "attempt to attach a particular whistle to a definite situation" (Caldwell and Caldwell 1965: 434) was never validated. "Lilly (1961*a*) may have been the first to hypothesize about the functions of specific dolphin whistles when he wrote of a distress call and an attention call... [With respect to the distress call] Lilly accurately described a widely generalized one-looped whistle of the species, but he assigned to it a specificity and uniqueness of context which was not tested. The evidence for both a context-specific distress call and a complex repertoire of context-specific whistles is weak" (Caldwell *et al.* 1990: 206).

Brain and acoustics research brought Lilly respect in the 1960s: he was an invited participant at the First International Symposium on Cetacean Research (Lilly 1966), and his reports were published in prestigious journals such as *Science* (*e.g.*, Lilly and Miller 1961*ab*; Lilly 1963*b*, 1965). An acknowledged expert on communication with extraterrestrial life (Wooster *et al.* 1966), Lilly's ideas about interspecies communication were taken seriously in the heyday of space exploration with funding from federal agencies such as National Science Foundation, National Institute of Mental Health, Air Force Office of Scientific Research (Lilly 1967*a*). Ridgway (1987: 10) recalled the persuasiveness of Lilly's argument "that scientists should learn how to communicate with dolphins to prepare for communication with intelligent life in outer space. Knowing of the dolphin's large, highly convoluted brain..., many scientists were taken with Lilly's ideas ...in the beginning."

These, however, were not the accomplishments that so profoundly influenced studies of cetacean behavior. "These useful, early contributions were followed by a series of books in which Lilly... extended his real findings into claims that dolphins possessed a language and that some, such as the sperm whale, possessed an intelligence whose complexity far exceeded our own. [These claims] extended the hope of interspecies communication between humans and dolphins" (Norris 1991*b*: 298). Cetologists became increasingly critical as Lilly failed to produce tangible evidence to support his ideas (*e.g.*, Caldwell and Caldwell 1965; Wood 1973). Extensive research by Caldwell *et al.* (1970: 12-3) refuted Lilly's claims, demonstrating that "the message content of dolphin whistles is simple and redundant rather than complex and specific. We found no evidence indicating a 'song patterning' or 'language'. The level of information content in the whistle may ...even exceed that of other advanced social animals but is much inferior in specificity to even a rudimentary language." Prescott (1981: 130-1) added that "...Dr. Lilly's initial results were no more than mimicry... Nearly simultaneously, utilizing the same training techniques... an obscure dolphin trainer [at Ocean World, Florida] stumbled upon the ability of dolphins to mimic human sounds... Unlike Lilly, this trainer realized that he had shaped a dolphin's behavior... and incorporated the result into a basic animal performance, leaving only the audience to misinterpret the results." Cetacean biologists became all-the-more dismayed when Lilly's focus shifted to altered states of consciousness, including experimentation with effects of a psychedelic drug on dolphin behavior (Lilly 1967*b*).

Disapproval also came from biologists studying other taxa. Entomologist and sociobiologist E.O. Wilson (1975: 474) denounced Lilly's books, *Man and Dolphin* (Lilly 1961*a*) and *The Mind of the Dolphin: A Nonhuman Intelligence* (Lilly 1967*a*), as "possibly the most widely read books on sociobiology and therefore ...extraordinarily misleading to both the general public and a wide audience of scientists." In his critique of *Man and Dolphin*, Wilson (1975: 474) wrote:

"Although Lilly never states flatly that dolphins and other delphinids are the alien

> intelligence he seeks, he constantly implies it... Anecdotes are used to launch sweeping speculations... Objective studies of behavior under natural conditions are missing, while 'experiments' purporting to demonstrate higher intelligence consist mostly of anecdotes lacking quantitative measures and controls. Lilly's writing differs from that of Herman Melville and Jules Verne not just in its more modest literary merit but more basically in its humorless and quite unjustified claim to be a valid scientific report."

Wilson (1975: 474) said that he "dealt frankly with these two books [because a] noncommittal attitude only serves to perpetuate the myth that Lilly helped to create."

If Lilly helped to create a myth, it was eagerly embraced and promoted by many others. Scientific disclaimers did little to diminish the public fascination with possibilities for communication with "an alternate sentient being -- benign, philosophical, and gifted with the patience and wisdom of the sea" (Parfit 1980: 73). Lilly charmed the public with his popular books and his self-portrayal as the only one "willing to stick his neck out" in defiance of narrow-minded scientists (Lilly 1961*a*: 135). Captivation with the promise of cetacean language and intelligence was also fanned by numerous nonprofessional publications, including pseudo-scientific books (*e.g.*, Stenuit 1968; Fichtelius and Sjolander 1972) and feature articles in such magazines as *Life* (Lilly 1961*b*; Schulke 1961) and *The Saturday Evening Post* (Appel 1964). A blockbuster novel, *The Day of the Dolphin* (Merle 1969), which was loosely based on Lilly's life and ideas (according to Lilly (1978)), was widely misconstrued as factual (Wood 1973). "[I]n recent years the authors of one popular book after another have *started* from the basic premise ...that the cetaceans represent a high order of ...intelligence. Human nature and the press being what they are, some of these accounts have received wide publicity... to the extent that complex dolphin sociology and high cetacean intelligence have joined motherhood and apple pie in the public mythology" (Gaskin 1982: 115).

The status of cetaceans as "floating hobbits" (Pryor and Norris 1991*b*: 2) was clinched with the 1963 hit movie, *Flipper*, which formed the basis for a long-running

television series and a resurrection of the film in 1996. "Even the Soviet government embraced an idealized image of the porpoise...[announcing in 1966] a ban on the catching and killing of porpoises... [because] extensive research both in Russia and abroad had shown that the porpoises' brain power makes them 'marine brothers of man'" (Wood 1973: 7). Public infatuation with cetaceans went so far as to promote dolphins as "the status pet... you can enjoy in your own swimming pool..." (Ciampi 1964: 22). Deploring the huge impact of Lilly's ideas, Wood regretted having been the one to introduce Lilly to dolphin vocalizations: "I'm not sure if I hadn't played him the tapes the world would be a different place now" (Parfit 1980: 74).

Wood's lament may well have referred to the damaging effect of Lilly's work on *bona fide* cetological research. Lilly's ideas were popular even to the extent of obstructing scientific progress. For example, "the important discovery that each dolphin has a unique acoustic signature, first reported [in Caldwell and Caldwell 1965], languished while many embraced the more fashionable view that dolphins had a complex language and that it was only a matter of time before researchers could decode it" (Leatherwood 1991: 98). Reeves (1983: 709) worried that negative reactions to Lilly's ideas might be counter-productive: "...I wonder if [Gaskin (1982)] hasn't over-reacted to some of the anthropomorphisms and sentimentalisms, in the process becoming not only provocative but defeatist. After all, ...serious questions about cetacean intelligence and social structure do not deserve to be dropped entirely just because a few investigators have approached them irresponsibly." The scientists from other disciplines who looked askance at Lilly's work similarly regarded with suspicion the cetacean biologists whom they considered Lilly's colleagues, asking "Can you be a serious scientist if you work with dolphins?" (Norris 1991*b*: 298).

Few contemporary discussions of cetacean intelligence credit (or even mention) Lilly's ideas, and few cetologists care to be linked with the name of Lilly. Nevertheless, Lilly's initial work set the stage for productive, legitimate scientific inquiries into

cetacean communication and cognition (*e.g.*, Richards *et al.* 1984, Richards 1986; Tyack 1986*b*; Caldwell *et al.* 1990). Unfortunately, Lilly's influence has also lived on in an unwavering public mythology that continues to bias perceptions of scientific studies of cetacean behavior.

A decline in contributions from zoo and aquarium research

> *"The establishment of a stable colony, which would be very helpful for research into the behavior of these animals, has not been considered necessary to produce a good exhibition group."* Margaret Tavolga 1966: 728

> *"[I]nterpretation of behavior observed in captivity must be approached with great caution. Moreover, captive bottlenose dolphins display a marked propensity to learn complex behavior sequences by imitation... and thus studies of their behavioral repertoire are fraught with further possible pitfalls of misinterpretation."* Graham S. Saayman and Colin K. Tayler 1979: 166

After several decades of productive research in zoo and aquarium settings, there has been a virtual hiatus in captive studies of cetacean social behavior since the 1970s (but see, *e.g.*, Overstrom 1983; Wells 1984; Tyack 1986*b*; Östman 1991; Samuels and Gifford, in press). No single, definitive cause has been named for this decline; rather, the evidence points to a suite of factors. Le Boeuf and Würsig (1985: 143) suggested an economic explanation, that "conducting marine mammal research in the lab is much more costly today [than a few decades ago] in large part because of the legal husbandry requirements... Consequently, outside of commercially self-sustaining oceanaria, not much behavioral work is being done on captive animals..." This interpretation, however, fails to explain why research on cetacean social behavior has similarly declined in zoos and aquaria or why captive research on cetaceans now emphasizes sensory systems over social behavior.

Transformation of the general character of zoo and aquarium research may be a contributing factor. At the time that captive cetacean behavioral studies were flourishing,

behavioral research in general was thriving in zoo environments (*e.g.*, Morris 1966; Kummer and Kurt 1965; Rabb *et al.* 1967). Indeed, "nowadays, many influential biologists owe much of their interest in biology to early experiences of animals in zoos, and this is particularly true of ethologists" (Robinson 1991: 120). Zoo-based research, however, has progressively moved away from studies of social behavior and moved towards "high-tech" applied research, particularly in genetics (Kleiman 1992; Thompson 1993). Nowadays, behavioral research in zoos and aquaria is typically driven by the needs of collection management and wildlife conservation (Kleiman 1992; Wemmer and Thompson 1995). Kleiman (1992: 310) worried that "zoos will be making a major mistake if they totally abandon more classical descriptive behavioral research and basic behavioral research..." This loss has already been felt in studies of cetacean social behavior.

For cetaceans, it seems likely that the decline in zoo-based behavioral research was also part of Lilly's legacy. In the late 1960s, Lilly became a staunch opponent of maintaining cetaceans in captivity, and he closed his dolphin lab, saying "...I began to see the ethical implications of my beliefs about dolphins. If what I believed about dolphins was true, I had no right to hold them in a concentration camp for my scientific convenience" (Keen 1971: 77). Lilly was inspirational to animal activist movements proliferating in the 1970s (*e.g.*, O'Barry and Coulbourn 1988), and the burgeoning anti-captivity stance was no doubt strengthened by the wide publicity accorded to the beliefs of a man of Lilly's stature (*e.g.*, Keen 1971; Hussain 1973).

Public attraction to cetaceans, engendered in part by oceanarium displays, also served to fuel animal activist efforts. For example, the killer whales' fearsome image was rendered more benign as the public gained access to whales in captive exhibits. Whereas previously, "Navy training films portrayed killer whales as dangerous vermin that might attack lifeboats and swimmers [and] some military fliers reportedly used them for bombing practice" (Pryor and Norris 1991*c*: 383); Newman (1994: 160) was able to

report "how quickly attitudes towards killer whales have changed over the decades since we captured Moby Doll in 1964. After years of people seeing ...[killer whales], there is a distinct social revulsion against shooting them..." This positive change in public opinion had the additional effect of fostering anti-captivity sentiments: "Many ordinary citizens became uneasy about [live-captures of killer whales] and began to press for regulation of the numbers captured" (Newman 1994: 155; see also Bigg and Wolman 1975).

The public also became critical of scientific research conducted with captive cetaceans. Scientists were was tainted in the eyes of some by a presumed association with pseudo-scientist Lilly, while they were distrusted by others for contributing data to the anti-captivity debate (Anon. 1984). In the U.S., additional suspicion of the scientific profession came from a coupling in the public eye of captive dolphin research with military efforts and the much-hated Vietnam war. The public was told that "[dolphin] research has passed from those with broad interests and a love of the animals [like Lilly] to scientists with narrow interests and US military money... The dolphin has become just another experimental animal, but one which conveniently can be trained to perform military tasks and dolphinaria tricks" (Hussain 1973: 182). Long forgotten were Lilly's own failures to resuscitate his dolphin subjects (Lilly 1961*a*), the military dollars that sustained his early research (Lilly 1967*a*), and his willingness to dose dolphins with psychedelic drugs (Lilly 1967*b*). Even though Lilly later softened his position and resumed research with captive dolphins (Lilly 1978), scientists in general remained *personae non grata* at many oceanaria.

These sentiments came on top of an already uneasy partnership between scientists and members of the public display community. Pryor (1975: 2) admitted that, even in early oceanarium days, "Public exhibits and private research didn't mix well. Experiments sometimes detracted from exhibits, and the scientists on the staffs of these oceanariums told horror stories of precious research animals being pressed into public

shows just when the data collecting was getting good." Marineland of the Pacific's first curator, Norris (1974: 99), recalled having conflicting views about his own research: "[T]he housekeeping for a porpoise is expensive; their tanks must be kept clean and supplied with running sea water, and they eat a dozen or more pounds of fish every day, so it is wasteful to have nonproductive [*i.e.*, nonperforming] porpoises at an oceanarium."

Even when it was possible to gain access to dolphins for research purposes, some scientists worried that aspects of captive conditions -- such as atypical group composition, human-animal bonds, training, sensory deprivation, and/or restricted space -- might distort natural social behavior (*e.g.*, Gaskin 1982). Those beliefs were part of a broader debate between animal psychologists and ethologists: "Ethologists have traditionally supposed the effects of captivity to be distorting [whereas] psychologists have supposed them to be innocuous or helpful" (Boice 1981: 407). Lorenz (1981: 47-8) further subdivided his fellow ethologists into the "hunter type" (like Tinbergen) whose preference for fieldwork derived from "the joy of stalking and lying in wait for animals, in short, by the pleasure of 'outwitting' them" *versus* the "herder type" (like Lorenz) who liked breeding and handling subjects for close-range studies.

Wood (1986: 332) responded to this controversy with a checklist for assessing the suitability of a given captive situation: "These are, of course, well-founded concerns. However, the competent student of dolphin behavior will take into consideration the quality of the captive environment. Does it provide some simulation of natural conditions...? Is the dolphin colony relatively stable and do births occur regularly? Does the behavior of the animals appear unstressed and natural, as opposed to stereotyped and with indications of boredom?"

How do social conditions at oceanaria stand up to these concerns? Are colony compositions appropriate? Predicting that Marine Studios would be the last colony in

which dolphins remained together on a long-term basis, Tavolga (1966) lamented the loss of stable social groups to cetacean behavioral research. Saayman and Tayler (1979: 165) confirmed her fears, complaining that shows often dictated group compositions to the extent that "...dolphins unresponsive to training procedures [were] generally rejected, and the colony therefore [did] not contain representative samples of animals." Saayman and Tayler (1979: 165) further noted that "the age/sex ratios of normal populations of dolphins are not known and therefore cannot be duplicated in captivity." Although much has since been learned about wild societies of cetacean species that are commonly held in captivity (*e.g.*, bottlenose dolphins: Wells *et al.* 1987; Scott *et al.* 1990*a*; Connor *et al.* 1992; Smolker *et al.* 1992), it remains true that captive colonies seldom resemble the composition or stability of species-typical groupings in the wild (Samuels, in press). For example, it is rare in bottlenose dolphin colonies that mothers and their calves remain together for as many years as their wild counterparts, that males are maintained as bonded pairs, or that female kin groups remain intact (but see, *e.g.*, Messinger *et al.*, in press).

Do births occur regularly? Do animals live long lives? "Some... have suggested that survival in captivity is substantially lower than what may be expected in the wild for some species (Klinowska and Brown 1986); however, such estimates... are often calculated from incomplete and/or disparate data sets using a variety of analytical techniques" (Small and DeMaster 1995: 209-10). For bottlenose dolphins, significant improvement in captive survival has been demonstrated in recent years, and despite differences among institutions, demographic parameters such as survivorship now compare favorably with those in the wild (DeMaster and Drevenak 1988; Small and DeMaster 1995). Duffield and Wells (1991: 15) found that "the values for reproductive parameters in the captive dolphin population exceed those of the wild population", and they concluded that "the maintenance and breeding of this species in captivity has been a success story." Annual survival rates for other captive species such as killer whales have also improved but still fall below rates in the wild (Small and DeMaster 1995).

Do animals exhibit species-typical behavior? There has been little systematic evaluation of differences in the behavior of captive and wild cetaceans. Cetaceans in certain captive conditions may manifest aberrant behavior (*e.g.*, Sweeney 1990); however, there is currently little basis for Pilleri's (1984: 15) insistence that "...it is perfectly well known that dolphins... which in the wild have no pecking order, suddenly turn savage in captivity..." In contrast, some scientists have recognized that in naturalistic environments "social interactions observed among captive animals may reflect, at least in part, the kind of social organization that could exist in the wild" (Tavolga 1983: 4-5; see also, *e.g.*, Pryor and Kang 1980; Samuels, in press). For example, Saayman and Tayler (1977: 113) noted: "Whereas it is well recognized that captive conditions may elicit atypical behavior... the high rates of copulatory activity observed in free-swimming dolphins... suggest that high levels of sexual behavior [observed in this captive study] are characteristic of the normal social interactions of these marine mammals." Similarly, Samuels and Gifford (in press) observed that "the [zoo] dolphins' social behavioral repertoire... resembled, nearly behavior for behavior, that of wild *Tursiops* in Western Australia...", and their captive study revealed "patterns of [agonistic] behavior that conformed to current knowledge about bottlenose dolphin social structure." Captive *Stenella* species also exhibit many basic behavioral patterns seen in the wild (*e.g.*, Pryor and Kang 1980; Wells 1984; Johnson and Norris 1994). Tavolga (1983: 4) acknowledged that "confirmations of this sort are, regrettably, uncommon, but highly significant when available..."

Are there detrimental effects of handling by humans? Kleiman (1992: 308) observed that for zoo animals in general, "as a result of more rigid animal welfare requirements, it is likely that today's specimens are handled, examined, and manipulated more than zoo animals a decade ago... It remains to be determined whether, and how, such frequent manipulations interfere with expression of natural behaviors..." Although effects on behavior may not be known, the particularly close relationships of captive cetaceans with their human caretakers have certainly influenced perceptions of cetacean

behavior which, in turn, have probably biased judgment as to the relevance of captive studies. Unlike most zoo exhibits, public display of cetaceans typically features trained behaviors and human-with-cetacean interactions (*e.g.*, Sea Life Park's porpoise-powered diver (Pryor 1975)) rather than natural behavior and dolphin-with-dolphin social relations. The human-focused perspective on cetacean performers has led to a blurring of distinctions among oceanarium staff, the public, and even scientists, between natural social behavior, human-with-cetacean interactions, and trained responses. These general misperceptions about the behavior of captive cetaceans have no doubt contributed to the paucity of captive studies of social behavior in recent years.

Wood's (1986) common-sense checklist suggested that behavioral observations made in captivity could be cautiously interpreted by taking the specific captive circumstances into account (see also, *e.g.*, Saayman and Tayler 1979; Johnson and Norris 1986; Östman 1991). Many cetacean biologists have nevertheless remained unconvinced as to the validity of captive studies, some apparently misinterpreting cautious explanations as denials of worth. Newman (1994: 199) recalled that "a schism had developed among marine mammal scientists, and it was very visible at [the Sixth Biennial Conference on the Biology of Marine Mammals in 1985]. The split was over the issue of aquariums and captive cetaceans. ...Ken Norris...represented the faction in the society that appreciated the value of captive cetaceans to the acquisition of scientific knowledge... [and particularly] in behaviour studies." The debate and its effects persist to this day.

One outcome of this long-standing controversy has been that areas other than social behavior have taken precedence in captive cetacean research. Specifically, "since the discovery of the echolocating capabilities of dolphins, most of the [captive] behavioral work has concentrated on the acoustic modality" (Tavolga 1983: 19). In the Navy's engineering approach to studying echolocation (*e.g.*, Au 1993), the presumed artificial effects of captivity have been no cause for concern. To the contrary, a controlled setting

is ideal for experimental tasks that are designed to reveal the extent of odontocete echolocational abilities rather than determine how animals actually make use of these capabilities. Such studies have demonstrated, for example, that "trained bottlenose dolphins can detect the presence of a 2.54 cm solid steel sphere at... nearly a football field away (Murchison 1980)... [and] can discriminate targets that are identical in terms of shape and differing only in composition (*e.g.*, Kamminga and van der Ree 1976)" (Tyack, in press).

Nevertheless, a stalwart few have maintained the belief that a dialogue between field and captive efforts holds "the key to understanding wild dolphins" (Pryor and Norris 1991*a*: 291; see also, *e.g.*, Saayman and Tayler 1979; Wells *et al.* 1980; Pryor and Kang Shallenberger 1991; Norris *et al.* 1994; Samuels and Gifford, in press). Saayman *et al.* (1973: 229-30) explained that "preliminary studies demonstrate the importance -- indeed, the necessity -- of simultaneously conducting complementary studies of animals under controlled captive conditions, where details of behaviour can be determined at close range, as well as under free-ranging conditions, where behaviour observed in captivity can be seen functioning under the appropriate socio-ecological circumstances..." Norris (1985: 7) voiced a similar viewpoint in a plenary paper at the Sixth Biennial: "A full understanding of the behavior of marine mammals requires studies both at sea and in captivity. Each provides a different view of behavior, and by working in both ways one may check and correct interpretation made in each."

These scientists appreciated the unique benefits of working in a controlled environment, including the ability to view cetaceans underwater and/or at close range, to observe entire sequences of behavior, and to monitor long-term the social relationships of known individuals. Such detailed, close-up observations have facilitated analyses difficult to achieve in the wild, for example, studies linking social behavior and hormones (*e.g.*, Wells 1984) or studies evaluating the functional significance of specific social behaviors (*e.g.*, male-female sexual behavior: Puente and Dewsbury 1976; male-

male sexual behavior: Östman 1991; agonistic behavior: Samuels and Gifford, in press). In addition, glimpses of social behavior at sea were sometimes better understood in light of intensive viewing of the same interactions in a captive setting (*e.g.*, Saayman and Tayler 1979; Pryor and Kang Shallenberger 1991). For instance, in their behavioral study of dolphins trapped in tuna nets, Pryor and Kang (1980: 74-5) noted that "experience with spotters and spinners in captivity was fundamental to observation in the nets. Virtually all of the behavioral events... were well-known to us from captive animals... Our familiarity with individual behavioral patterns, as evidenced by the preparation of a very adequate 'dictionary' before going to sea, allowed us to identify actions which might be indecipherable to a novice observer."

Caveats, qualifiers, and accolades notwithstanding, it remains true that, since the 1970s, zoo-based studies of cetacean social behavior have been virtually nonexistent. As unfortunate as this lapse is for a better understanding of the social behavior of small cetaceans, captive research has played a significant role in promoting another major phase of cetacean research: field studies. In the 1970s, some cetologists took their cue from the experience of primatologists, many of whom were shifting towards field research. At the time, Evans and Bastian (1969: 470-1) noted that:

> "[T]he current state of [cetacean behavioral research] is very reminiscent of the recent history of primate behavior studies. Popular interest has long supported public display of captive primates in much the same way that the cetacean... displays now enjoy the public's fancy. But although much was written about primate social behavior based on close observation of these captive groups, a large part of the ideas that resulted from these efforts has been forced to be drastically revised. The recent flourishing of ecologically sophisticated studies of free-ranging populations that has been the happy lot of behavioral primatology has provided a much deeper and fuller understanding of the social life of these animals... Our fervent hope is that the same history will unfold in the study of the social behavior of marine mammals."

Norris recalled that it was not only the limitations but also the exciting discoveries of captive research that inspired cetologists to take the next step into field work: "From the first few captives in oceanariums, we began to understand that these cetaceans were

complex mammals many of whose behavior patterns bore a startling resemblance to those of terrestrial mammals. So a few people... began to grapple with learning about dolphins at sea" (Pryor and Norris 1991*c*: 385).

Studies of free-ranging cetaceans, discussed below, have enhanced our understanding of cetacean social organizations. However, as we become better informed about social structure, we realize how much is yet to be learned about social behavior and social dynamics. Investigation of those phenomena will sometimes require the close-range, detailed observations that may be best accomplished in naturalistic captive settings. Thus, armed with greater knowledge about societies of small cetaceans, improved conditions in oceanaria, and Wood's (1986) guidelines, it may be timely to resume studies of the social behavior of small cetaceans in zoo and aquarium environments and thereby renew the dialogue between captive and field studies.

FIELD STUDIES

"No longer must we kill whales to study them" [5]

> *"These new [passive observational] approaches are bound to bring new understanding. Far from nurturing the growth of knowledge in whale biology, I feel that the availability of large numbers of corpses, and thus the possibility of more years of the old study methods, has actually held back the growth of this branch of science."* Roger Payne 1983: 3

> ***"Megaptera novaeangliae** is a species in which minor individual variations are often sufficiently conspicuous and distinctive to enable even a shipboard observer to recognize individual whales..."* William E. Schevill and Richard H. Backus 1960: 279

By the 1960-70s, many cetologists had come to conclude that only limited

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[5] Darling 1988: 872

deductions could be made about the social behavior of cetaceans if observations were not conducted on living animals in the natural environment. Those who embarked on field studies of small cetaceans were inspired (both positively and negatively) by captive studies. Opposition to a traditional reliance on carcass analyses sent other cetologists to sea to study the larger whales. McVay (1974: 381) felt strongly that "cetology has for a long time been a 'dead' science... [T]he bulk of the scientific reports are based on data taken from dead whales and those data consequently are industry dependent. This means that, wittingly or unwittingly, the whale scientist may often be in a parasitic relationship to the whaling industry... [W]hat has been missing from the equation has been any systematic study of the whole organism and its relation to group and environment." In the same vein, Payne (1983: 2) rejected the idea that "serious science cannot be done without dead whales...", a stance he believed to be fostered by the whaling industry to garner continued support for whaling. As an alternative, Payne (1983: 1) proudly presented an edited volume, *Communication and Behavior of Whales*, the studies in which were "all based on passive observation techniques. There is no result in this book that was derived from killing, capturing, confining, or even touching a whale... [which demonstrates] that basic science can be done at a useful level of rigor... without resorting to intrusive techniques or commercial whaling operations."

The anti-cadaver movement in cetology was long preceded by similar sentiments in other animal studies. At the turn of the century, ornithologist Selous "declared war on all previous ornithological writing" (Stresemann 1975: 342), stating that: "The zoologist of the future should be a different kind of man altogether: the present one is not worthy of the name. He should go out with glasses and notebook, prepared to see and to think. He should stalk the gorilla, follow up the track of the elephant, steal up on the bear... but it should be to biographise these animals, not to shoot them...

> Some men have strange ambitions. I have one:
> To make a naturalist without a gun" (Selous 1905: 323).

By the 1920s, many ornithologists reacted against carcass studies: "We are concerned

here not with the study of skins... but rather with subtleties of behavior, with growth and development, with molting, with instinctive actions and mental abilities -- in short, with matters that up to now have been scarcely considered" (O. Heinroth, quoted in Stresemann 1975: 348). Allee (1933: 320) made a similar remark in his review of Bingham's (1932) monograph, *Gorillas in a Native Habitat*: "[A]t last such field studies have been put on a sound basis which should result in the hunting of information rather than of specimens."

Admonishments like these led to "a new generation of Dutch and German ornithologists [and zoologists] that soon became the leading investigators of behavior" (Stresemann 1975: 348); these were the classical ethologists of the 1930-40s. "Classical ethologists were careful observers who were more concerned with the observation and description of behavior under natural conditions than with the formulation of complex theories. To use Tinbergen's label (1958), ethologists were 'curious naturalists'" (Dewsbury 1984: 10). By the 1950s, modern ethology emerged as the classical form blended with such disciplines as ecology, comparative psychology, and physical anthropology (Hinde 1966; Dewsbury 1984).

Perhaps because of the lucrative influence of whaling, or perhaps because "at first, we cetologists literally did not know whether behavioral studies... in the wild were possible..." (Pryor and Norris 1991*c*: 385), it was not until somewhat later that cetacean biologists were able to replace carcasses studies with research on live animals in the natural environment. Caldwell (1955) and Schevill and Backus (1960) were the ones who set the stage for studies of free-ranging cetaceans by demonstrating that a bottlenose dolphin and a humpback whale, respectively, could each be identified over a period of days while alive and at sea. These studies established that it was possible to obtain information about the behavior and ranging patterns of whales and dolphins in the wild. Many cetologists followed this lead, and cetology increasingly came to emphasize non-lethal methods for studying free-ranging animals. Norris (1991*a*: 9) recalled early field

studies of small cetaceans:

> "[B]y the late 1960s, a few Western naturalists had hitched up their field pants and begun to seek out the best means and the best places to observe wild dolphins. They chose sea cliffs, they developed little radios that could be affixed to dolphin fins, and they began to watch dolphins underwater.
>
> Probably the first concerted attempt was that of the South African team of Graham Saayman and C. K. Tayler. Saayman, a primate biologist, knew that one way to study social behavior was to start recording patterns, whatever one can see; in time, from the arid precincts of one's recorded measurements and numbers, an understanding might emerge... Their work... revealed tantalizing hints of schoolwide cooperative fishing methods by the bottlenose dolphin."

Calling the movement toward field research "a fresh breeze", McVay (1974: 381) singled out other exemplary efforts: "While attention to the natural history of cetaceans is not new, the beginnings of a stronger orientation toward living cetaceans are found in such work as the phonograph [record]... produced by Schevill and Watkins in 1962. Scientists are now determined to know the whale in its natural habitat of the sea..."

These early fieldworkers not only launched studies of free-ranging cetaceans, but perhaps more importantly, they demonstrated that it was possible to repeatedly find and recognize naturally-marked, individual cetaceans on separate occasions. Schevill and Backus (1960: 279-80) observed the same humpback whale on seven days of a ten-day cruise, noting that "our subject was readily distinguishable by its larger size, by the shape of the dorsal fin or hump (especially variable in this species), and by the distinctive color pattern of the underside of the flukes (markedly unlike any of the others with it)."

This realization came at about the same time as similar awareness for many terrestrial mammalian species. Until that time, for most species, cetacean or otherwise, "artificial marking and tagging was considered almost a prerequisite for behavioral work..." (Würsig and Jefferson 1990: 43). Artificial tagging, pioneered with successful bird banding in the late 19th century (Delany 1978), continued to be used in most bird studies (but see, *e.g.*, Scott 1978). However, it became well-known in primate field

studies that "monkeys and apes tend to show so much variation in their facial and other features that numerous individuals can be recognized" (Schaller 1965: 628). Thus, Schaller (1963) kept track of individual mountain gorillas by making a collection of "nose-print" diagrams, and van Lawick-Goodall (1971) was able to identify each chimpanzee by unique facial characteristics. Animals other than primates were also found to be individually distinctive: the Douglas-Hamiltons (1975) recognized African elephants by looking at tusk shapes and ear outlines, and Pennycuick and Rudnai (1970) discovered that lions could be precisely discriminated by patterns of vibrissa spots. The unique striping patterns of plains zebras were detected by the Klingels (1965), who were leaders in the development of photo-identification techniques (Moss 1975).

Since the Discovery Investigations of the 1920s, individual whales had been monitored by means of artificial tags to obtain estimates of population parameters and to detect migration patterns; these tags, however, were internal and could only be recovered when marked whales were killed (Brown 1978). Many cetologists felt it was time to replace the Discovery marks and "consider other means of carrying out research on large whales... without killing large numbers of animals" (Brown 1978: 73). The work of Caldwell, Schevill and Backus offered promise that for some cetacean species, individual recognition might be accomplished by non-invasive means.

The idea caught on quickly. "[T]he extensive use of natural marks [to identify individuals] began for four odontocete species in five widely separated projects all within a two- or three-year period... [at the same time as individual] recognition of humpback whales... and Southern Hemisphere right whales..." (Würsig and Jefferson 1990: 43). One of the pioneers, Payne (1995: 63), remembered preliminary stages of the southern right whale project at Peninsula Valdes, Argentina: "I guessed that by photographing the heads of all the whales from the air we could create a 'head catalog' of known callosity patterns and thereby keep track of individual whales over long periods. In 1971 we demonstrated that this was indeed feasible but more time had to pass before we were

finally sure that the patterns were constant enough to be used in identifying right whales throughout their lives." Bigg (1994: 14), another leader, described a similar realization about photographing killer whales of the Pacific Northwest: "The pictures revealed several individuals with distinctive nicks and gouges on their dorsal fins. This provided us with natural identification tags... We had now discovered a method to study killer whales and could begin documenting the life histories of many individuals."

Thereafter, many cetacean field workers learned to discriminate the often subtle natural markings that distinguished individual whales and dolphins (reviewed in IWC 1990). In addition to distinctively-marked dorsal fins and saddle patches of killer whales (Bigg 1982); the characteristic callosity configurations on heads of southern right whales (Whitehead and Payne 1981; Payne *et al.* 1983); and the distinguishing color patterns on ventral surfaces of humpback whale flukes (Katona *et al.* 1979; Katona and Whitehead 1981), individuals of other cetacean species have been recognized in various ways, including identifying marks on the trailing edge of sperm whale flukes (Whitehead and Gordon 1986); unique combinations of dorsal fin markings and back pigmentation of minke whales (Dorsey 1983; Dorsey *et al.* 1990); and the nicks, notches, and shapes of dorsal fins of bottlenose dolphins (*e.g.*, Irvine and Wells 1972; Würsig and Würsig 1977; Shane and Schmidly 1978), humpback dolphins (Saayman and Tayler 1979), and spinner dolphins (Norris and Dohl 1980*a*). For some species, individual recognition was enhanced and its validity confirmed by artificial marking techniques such as visual tags and freeze-branding (*e.g.*, bottlenose dolphins: Irvine *et al.* 1982).

Thus, since the 1970s, "individual identification has indeed become a staple of field research" (Würsig and Jefferson 1990: 43), for marine and terrestrial species alike. The ability to recognize individual animals repeatedly over periods of years ushered in an era of long-term field research. Wells (1991: 201) recalled that "when our research program [on bottlenose dolphins in Sarasota waters] began in 1970, it was not planned with the intention that it become a long-term study." However, he and his associates

learned that "conclusions based on short-term data tend to be simplistic and transitory. Collecting data for only 2 or 3 years is unlikely to give a complete picture of a complex society of long-lived animals..." (Scott *et al.* 1990*a*: 242).

Longitudinal studies of many terrestrial mammals were initiated in the 1960-70s, and some have been continuous to the present (*e.g.*, chimpanzees: Goodall 1965, 1986; baboons: Altmann and Altmann 1970; Altmann 1991; lions: Schaller 1972; Packer *et al.* 1988; elephants: Moss 1977, 1988). This list also includes longitudinal, terrestrial studies of marine species such as elephant seals (*e.g.*, Le Boeuf and Peterson 1969; Le Boeuf and Reiter 1988). At the same time, several field studies of cetaceans were begun, many of which have been ongoing since their inception (*e.g.*, bottlenose dolphins: Irvine and Wells 1972; Scott *et al.* 1990*a*; Wells 1991; killer whales: Bigg 1982; Balcomb *et al.* 1982; Ford *et al.* 1994; spinner dolphins: Norris and Dohl 1980*a*; Norris *et al.* 1994). Payne (1995: 102) exulted in the returns from 25 years of studying right whales: "[W]e now know over twelve hundred individual right whales. We are expecting our third generation of calves -- descendants of mothers we first met back in 1970, many of whom are still alive and still in their calf-bearing years."

During the same period, the field of animal behavior came into its own: the Animal Behavior Society was organized in 1964, a number of professional journals were established (*e.g.*, *Aggressive Behavior*, *Hormones and Behavior*, *Behavioral Ecology and Sociobiology*), and many animal behavior textbooks were published (*e.g.*, Dewsbury and Rethlingshafer 1973; Alcock 1975; Wilson 1975; Colgan 1978). In 1973, the contributions of ethology were honored when Konrad Lorenz, Niko Tinbergen, and Karl von Frisch were awarded the Nobel Prize, an "event [which] provided inspiration for all animal behaviorists" (Dewsbury 1984: 11).

Kodachrome, hydrophone, and a "semisubmersible seasick machine" [6]

> *"It is obvious that no matter where and how it is studied, the whale requires the application of a wide range of innovative methodologies and techniques..."* Howard E. Winn and Bori L. Olla 1979: xii

Cetologists had to devise ingenious methods to monitor their elusive subjects. Many investigative techniques that would become standard were added to the researchers' toolkit during the early field efforts. However, with the near-simultaneous proliferation of several field projects in the 1970s, it is difficult to pinpoint who first developed or applied which technique. It is widely acknowledged that Roger and Katy Payne and their colleagues were especially influential in introducing, adapting, and validating a number of methodologies for studying cetacean behavior at sea; therefore, a review of procedures implemented during initial fieldwork at Peninsula Valdes provides a sampler of research techniques still routinely employed in cetacean field biology today.

In studies of bottlenose dolphins at Peninsula Valdes, for example, the Würsigs were among the first to apply to cetaceans the photographic technique for recording individuals by their natural markings (Würsig and Würsig 1977), a method now used in nearly all cetacean field studies (*e.g.*, IWC 1990; and references above). They extended this procedure to obtain measurements of group stability (Würsig and Würsig 1977; Würsig 1978) and to evaluate preferential associations of individuals (Würsig 1978). These methods have been replicated or adapted in studies of many cetacean species, including killer whales (*e.g.*, Heimlich-Boran 1986), bottlenose dolphins (*e.g.*, Wells *et al.* 1987), and sperm whales (*e.g.*, Whitehead and Arnbom 1987; Whitehead *et al.* 1991).

The Peninsula Valdes researchers also experimented with ways to observe cetaceans from afar so as to eliminate reliance on sea-going vessels which can be

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[6] Norris and Wells 1994: 58; coined by W. E. Schevill (W. A. Watkins, personal communication)

disruptive to animals or restrictive to research budgets. For example, Roger Payne adapted use of a surveyor's theodolite to monitor movements of nearshore cetaceans from a clifftop vantage point, a method put to good use in the Würsigs' studies of dolphin behavioral ecology (Würsig and Würsig 1979, 1980) and in the Clarks' study of southern right whale communication (Clark and Clark 1980). The theodolite has become the tool of choice in research requiring precise records of the movements of coastal cetaceans (*e.g.*, Tyack 1981; Würsig *et al.* 1991). In addition, the observation of Payne *et al.* (1983) that southern right whales rarely reacted to circling aircraft led to use of small planes to obtain an overhead, big-picture view of whale behavior (see also Watkins and Schevill 1979). This technique is still commonly used in remote areas, for example, to monitor behavior of Arctic bowhead whales (Würsig *et al.* 1984, 1985, 1993) or to examine school structure of pelagic dolphins (Scott and Perryman 1991).

For longer range monitoring of movement patterns, radio-telemetry devices were adapted for cetacean research. "William Evans... was the cetologist most responsible for developing the dolphin radio tag that now allows us to follow dolphins at sea" (Norris 1991*a*: 9). Evans' own work was not conducted at Peninsula Valdes, but some of his preliminary tags were used there in studies of dusky dolphins (Leatherwood and Evans 1979; Würsig and Würsig 1980). Development of a radio tag for large whales began in 1961 (Schevill and Watkins 1966), and refinement of those devices has continued since that time (see, *e.g.*, Watkins and Schevill 1977*a*; Leatherwood and Evans 1979). Tagging and biotelemetry have been applied to learning about various aspects of cetacean lives, including the animal's "environment (*e.g.*, water temperature, salinity...), behavior (*e.g.*, diving depth, swimming speed, sound production), or physiological state (*e.g.*, heart rate, body temperature) as a function of time and location" (Leatherwood and Evans 1979: 2; see also, *e.g.*, Norris *et al.* 1974; Scott *et al.* 1990*b*; Würsig *et al.* 1991). Technological advances have made it possible to monitor the behavior of even the most elusive species, including harbor porpoises (*e.g.*, radio telemetry: Read and Gaskin 1985; time-depth recorders: Westgate *et al.* 1995; satellite telemetry: Westgate

and Read 1995); sperm whales (*e.g.*, acoustic telemetry: Watkins *et al.* 1993); and fin whales (*e.g.*, radio telemetry: Ray *et al.* 1978; Watkins *et al.* 1981; satellite telemetry: Watkins *et al.*, in press).

Also at Peninsula Valdes, sound playback techniques -- borrowed from investigations of bird songs and grasshopper calls (reviewed in Falls 1992) as well as seal sounds (*e.g.*, Watkins and Schevill 1968) -- were applied to studies of cetacean communication (Clark and Clark 1980). The Clarks' prediction that this method would prove "useful in determining the biological function of the sounds in a whale's acoustic repertoire" (Clark and Clark 1980: 664) has been confirmed many times over, as in evaluating the function of humpback song (Tyack 1983; Mobley *et al.* 1988) or bottlenose dolphin signature whistles (Sayigh *et al.* 1993). In addition, focal-animal behavioral sampling techniques (Altmann 1974) were introduced to cetacean field studies in observations of southern right whale mothers and calves from the cliffs of Peninsula Valdes (Taber and Thomas 1982; Thomas and Taber 1984).

Of course, Peninsula Valdes was not the only site where innovative ideas were being applied to field research. In studies of Hawaiian spinner dolphins, Norris and Wells (1994: 54) had long felt that: "A major challenge of the study of dolphin natural history is to place an effective observer under the water in the ocean where dolphins live out their life patterns." Underwater observations have been crucial in, for example, deciphering the gender and roles of singing humpbacks and their associates (Glockner 1983). Norris (1991*c*: 215), however, had dreams of more extended observations from beneath the surface, of being "like Captain Nemo sitting before his underwater picture window... [looking out on the dolphins'] lives from the comfort of [an] air capsule." Norris and colleagues built several incarnations of underwater viewing chambers: the prototype, with the unsettling nickname of "semisubmersible seasick machine" (Norris and Wells 1994: 58), enabled them to be the "first scientists to study [the dolphins'] wild societies underwater where their lives are truly spent" (Norris 1991*c*: 13). "[The]

underwater observational dimension... allowed us to observe [spinner dolphins] in the context of a wild school, complete with predators, food sources, and the physical world of the sea" (Norris 1994: 2), which led to the conclusion that "the [spinner] dolphin school, however fluid, was a social unit that enclosed and protected the life patterns of wild dolphins in three-dimensional space" (Norris and Wells 1994: 55-6).

Others had a different approach to "seeing" underwater: "In order to reach below the surface and try to assess the behaviors of submerged whales, we utilized underwater sound..." (Watkins 1981: 84). Techniques such as a "non-rigid three-dimensional hydrophone array" (Watkins and Schevill 1972) made it possible to track the movements (*e.g.*, Watkins and Schevill 1977*b*) and record the vocalizations (*e.g.*, Watkins and Schevill 1977*c*) of individual cetaceans underwater. "The sounds from finback whales... provided the stimulus for much of the early progress in design of equipment and techniques for acoustic observations at sea" (Watkins 1981: 84) because these whales turned out to be the source of the mysterious 20-cycle pulses (Schevill *et al.* 1964) that had long puzzled underwater listeners including geophysicists and the military. Watkins *et al.* (1987: 1901) later determined that "direct association of the [signals] with the reproductive season for this species points to the 20-Hz signals as possible reproductive displays by finback whales."

Nearly all methodologies illustrated above exemplify the prominence of "employing a team approach" (Scott *et al.* 1990*a*: 243) in cetacean fieldwork. Those studying bottlenose dolphins in Sarasota waters have "learned the value of simultaneously pursuing multiple lines of investigation... The study has become more and more of a corporate affair, uniting biologists interested in behavior, life history, genetics, acoustics, reproduction, and population biology" (Scott *et al.* 1990*a*: 243). Examples of special collaborative efforts in cetacean field research have been the partnerships formed by scientists with members of the public or whale-watch operators to locate, census, and/or photograph killer whales of the Pacific Northwest (*e.g.*, Bigg *et al.* 1990; Ford *et al.*

1994) or humpback whales of the Gulf of Maine (*e.g.*, Clapham and Mayo 1990; Katona and Beard 1990; Lien and Katona 1990; Clapham 1994).

Save the Whale [7]

> *"These projects... have grown out of a sense of the vulnerability of marine animals to anthropogenic changes in the marine environment... As top predators in marine food chains, seals and whales provide a complex signal, in terms of dispersion, abundance, reproduction, and survival, describing the state of the environment."* Ian L. Boyd 1993: 4

In addition to a role as indicator species for the well-being of the marine environment, the health of cetacean populations has long been of intrinsic interest. Management and preservation of cetacean populations has been a guiding force in cetology and a particular incentive for understanding cetacean behavior. Even though long-term field studies of marine mammals were established at nearly the same time as those for terrestrial mammals, the growing environmental consciousness of the 1970s was much more closely reflected in field research on cetaceans. For example, Payne (1980: 551) described his motivation for studying southern right whales:

> "To avoid [the extinction of] right whales, we need to know much more about them. In spite of 30 years of nominal protection, they have not undergone the rapid recovery in numbers that gray whales have... We have no idea why this may be so, so little is known about the basic biology of this species. Our aim in the research reported here was to study the basic biology of the right whale and to develop estimates of its population by new methods that would not rely on killing whales. The final phase of the work was to apply what we had learned to preserving the species."

Bigg (1994: 13) and his colleagues began studies of killer whales for related reasons, because "fisheries managers and the public were concerned about the live-capturing of killer whales for aquaria." Bigg (1994: 13) recalled:

"The study began in 1970 [when] biologists in British Columbia and Washington

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[7] 1970s anti-whaling movement (see, *e.g.*, Day 1987)

> State were faced with an urgent request... The questions posed concerned whether the removals were endangering the local killer whale population and what restrictions should be introduced if more whales were to be taken. This required knowing how many killer whales were in the region; whether the whales taken in Washington State were from the same stock as those taken in British Columbia; what the productivity of the population was; and whether the removal of one particular age or sex was detrimental to productivity. Little was known about these topics..."

Conservation and management have persisted as the principal research thrusts of cetology even though the threats have changed over time. The risks to large cetacean populations have diminished since the IWC adopted the worldwide moratorium on commercial whaling which took effect in 1986 (IWC 1983). Similarly, effects of live-capture on small cetacean populations in U.S. waters have declined since federal capture quotas were instituted in the 1970s (*e.g.*, in 1977 for bottlenose dolphins: NMFS 1990), and especially since zoos and aquaria discontinued live-capture of the most commonly-exhibited species, the bottlenose dolphin, in 1990 (NMFS 1993). "New threats have emerged, however, that are more subtle in their expression but perhaps no less significant. These include: incidental take during fishing operations; entanglement in lost and discarded fishing gear; disturbance by boats engaged in whale-watching and other activities; and habitat degradation and destruction due to fishery development, dumping, dredging, offshore oil and gas development and other human activities" (Hofman and Bonner 1985: 116).

In the U.S., conversion to a conservation focus involved more than merely a change in ideals; it became the law: "The Marine Mammal Protection Act of 1972 makes the United States government responsible for long-term management of marine mammal populations. This means conserving and protecting these populations and doing research on them to see that it is done wisely... The positive effects, from a scientific point of view, are that money is allocated for applicable research on phenomena important in managing populations" (Le Boeuf and Würsig 1985: 139).

Inevitably, where the research funding came from "greatly influenced whom we cetologists were talking to and what kinds of question we were asking" (Pryor and Norris 1991*c*: 385). Funds earmarked for estimating cetacean population parameters led to research priorities with a management focus. From a conservation perspective, such research was badly needed. And, as Le Boeuf and Würsig (1985: 139) pointed out, "although the research mandated appears to be closely tied to management's charge of keeping populations near optimal levels, the information gained is likely to be of general interest." Thus, for example, significant contributions to our knowledge about bowhead whale behavior were by-products of studies funded by the U.S. Minerals Management Service "to obtain information directly useful for management decisions regarding potential disturbance of whales through oil and gas industry activities..." (Würsig and Clark 1993: 157; see also, Würsig *et al.* 1984, 1985, 1993).

Many cetologists were already well-schooled in the necessary methods for deriving estimates of population size and reproductive rates as a result of their experience in whaling resource management. Now, however, the onus was on fieldworkers to demonstrate that new passive observational techniques could adequately provide the population-level statistics previously supplied by carcass analyses. Whitehead and Gordon (1986: 163) were able to demonstrate that "benign [non-invasive] research can duplicate the kinds of data provided by commercial whaling, as well as investigat[e] some areas of ...whale biology for which catch data could not provide information" (see also, *e.g.*, Whitehead and Payne 1981; Payne 1983). Once "it became clear that data on resightings of individuals could provide information on the abundance, survivorship, reproductive rates, and population differentiation of whales" (IWC 1990: v), the new-found ability to distinguish individual cetaceans was widely applied to calculations of population parameters.

This led to considerable interest in developing capture-recapture methods to approximate population and life history parameters based on resightings of naturally-

marked cetaceans (*e.g.*, Hammond 1986). An entire Special Issue of the IWC Report was devoted to this area of research with articles detailing photographic methods, field protocols, modelling and statistical techniques, and the advantages and disadvantages of using natural *versus* artificial marks to identify animals for population-focused analyses (IWC 1990). The high-level investment was due in part to the urgency of the conservation-based effort and in part to the perceived novelty of the enterprise: "Although the recognition of individual animals from natural markings is a common practice in behavioural studies, these data are rarely used for the estimation of population size. Apart from a study of alligators..., I know of no others of this kind except for those on whales..." (Hammond 1986: 254). This claim to distinction refers to the special problems associated with estimating population parameters from mark-recapture models based on naturally-marked animals. Demographic analyses of terrestrial mammals were also based on naturally-marked individuals; in those analyses, however, the population parameters were known, not estimated, because all individuals could be routinely monitored (*e.g.*, Clutton-Brock 1988).

As studies of social structure, social behavior, and natural history had been subsumed under resource management, they were now motivated and guided by conservation concerns. In 1982, an IWC-sponsored workshop was dedicated to identifying those "behavioural 'problem areas'" that would dictate revisions in assessment methods or management procedures (IWC 1986: 3). The workshop sought to identify "new areas of behavioural research which would materially assist future management of whale stocks" (IWC 1986: iii). Thus, behavioral studies of right whale calves (Taber and Thomas 1982; Thomas and Taber 1984) were used to illustrate the value of such longitudinal work to accurately estimate recruitment: "Without callosity identification we might have mistaken the yearlings returning to Golfo San Jose with their mothers as infants born out of the normal calving season... These yearlings acted superficially like infants, and did not appear to our eyes to be much larger than infants we had watched depart six months earlier. Without certain identification, we would have made incorrect

inferences about the range of the calving season and about mother-infant behaviour" (Thomas 1986: 118).

"Far from conventional mammals" [8]

> *"Unravelling the structure of a cetacean school and the functions that the school promotes requires long careful observations of wild aggregations."* Kenneth S. Norris and Thomas Dohl 1980*b*: 212

The take-home message was still relevant from the earlier efforts to adapt whaling models to the sperm whale's unconventional social structure: population parameters could not be accurately modelled unless the complexities of cetacean social organizations were better delineated. Armed with innovative field research techniques, fieldworkers made "long careful observations" in order to decipher cetacean social systems. These efforts resulted a wealth of detailed, longitudinal data from individual animals which, taken in composite, have begun to reveal the intricacies of many cetacean societies. For example, an outcome of long, careful observations of killer whales in the Pacific Northwest is that "all [261] members of the two communities of the resident form of killer whale... have been identified and monitored annually since 1973... [T]he study has provided a complete record of the number of viable births, deaths, and the total size of the two communities as well as information on the age, growth, maturity and calving histories of their constituent individuals" (Olesiuk *et al.* 1990: 210).

From this remarkable database, it was possible to tease apart several layers of killer whale society to discover that "killer whales were far from conventional mammals; indeed certain aspects of their biology appeared unique. Two different forms of the species -- residents and transients -- lived in the same waters, yet never associated and

[8] Ford *et al.* 1994: 8

seemed to specialize on different prey -- fish for residents and mammals for transients. The social structure of the resident whales was exceptionally unique, with young whales staying in their mother's group well into maturity and probably for their entire lives. Also, each resident killer whale pod was found to have a unique vocal dialect that appeared to encode its relationship to other pods in the population" (Ford *et al.* 1994: 8). Although living in cohesive, long-lasting groups based on matrilineal kinship (*e.g.*, Bigg *et al.* 1990) is not an uncommon mammalian social arrangement, the killer whale social system is unusual in several respects. Not only do "resident whales of both sexes [remain] in their natal pod throughout life" (Olesiuk *et al.* 1990: 211) but, whereas "different social systems [existing] within a species is not unusual..., it is unusual to find variations in social systems at the same place and time in one species, as exists in the resident and transient forms of killer whale" (Bigg *et al.* 1990: 398).

Deciphering bottlenose dolphin society has been somewhat more challenging. Early reports of the fluid nature of dolphin social groupings (*e.g.*, Würsig 1978) led Gaskin (1982: 151) to suggest that dolphin social structure was probably no more complex than it seemed, that "the [social] bonds are loose, and animals wander in and out of areas, or depart for good to seek new territories for feeding, because a society does not exist at all..." Many field seasons later, however, dolphin researchers had ample evidence to refute Gaskin's simplistic explanation (*e.g.*, in Sarasota: Wells *et al.* 1987; Scott *et al.* 1990*a*; Wells 1991; in Western Australia: Smolker *et al.* 1992; Connor *et al.* 1992). Sarasota fieldworkers have "since 1970... used capture-mark-and-release techniques and photographic identification to study bottlenose dolphins... As a result of these efforts, [they] can recognize nearly every member of a resident population..." (Wells and Scott 1990: 407-8). The long-term effort has resulted in another extraordinary data set that includes demographic and kinship information for nearly all dolphins in the community. Based on this information, the following picture has emerged of bottlenose dolphin society, at least in coastal regions: "The Sarasota community represents a relatively closed society... [Although] dispersal of young out of the community has not

yet been documented... short-term absences... have been recorded for maturing and adult males... This community of about 100 animals was composed of smaller assemblages of socially interacting individuals [which] were organized on the basis of age, sex, familial relationships, and reproductive condition. Groups of regular, long-term associates were generally of the same age and sex... [and] shared congruent ranges" (Wells *et al.* 1987: 291-2).

An unusual feature of coastal bottlenose dolphin society is that "temporary parties of flexible composition" on a day-to-day basis are combined with "strong adult associations among particular males and ...among particular females" over the longer term (Smolker *et al.* 1992: 64). Typically, "males formed pairs and triplets [with other males] that in many cases were together as consistently as mothers with their calves... A male subgroup associated with other dolphins in a fluid manner, but did so as a cohesive unit... [In contrast] the pattern of association in the female population was best described as a network in which almost every female was connected to all other females by a chain of consistent associates. Long-term female-female associations divided the network into cliques, which were relatively stable..." (Smolker *et al.* 1992: 59). Sarasota researchers believed "that adult female bands [cliques] comprise the stable core of the... community. The members of bands appear to be linked by genetic ties and by long-term associations stretching over years or even decades." (Scott *et al.* 1990*a*: 242). Aspects of bottlenose dolphin social structure have been variously compared to several terrestrial mammalian societies. Male alliances have been likened to those of chimpanzees (Connor *et al.* 1992) and lions (Wells *et al.* 1987); fission-fusion society, to that of chimpanzees or spider monkeys (Tayler and Saayman 1972; Würsig 1978; Smolker *et al.* 1992); and the matrilineal basis for female bands, to prides of lions (Wells *et al.* 1987).

Within these community-level frameworks, the social lives of individual whales and dolphins remain largely unknown. What kinds of relationships does a female sperm

whale have with members of her kin group or with members of other matrilineal groups? Is kinship a factor in determining the agonistic dominance relationships of female dolphins? What social roles are played by postreproductive female pilot whales? What are the social functions of signature whistle mimicry by bottlenose dolphins? Questions like these, and many more, remain to be answered.

"Individuals ...armed with many behavioral options" [9]

> *"Those who have never attempted to measure behaviour may suppose from the safety of an armchair that the job is an easy and straightforward one, requiring no special knowledge or skills. Is it not simply a matter of writing down what happens?"* Paul Martin and Patrick Bateson 1994: 2-3

> *"Individual recognition of animals is essential in a detailed study of social behavior."* George B. Schaller 1965: 628

It was ornithologists who first realized the significance of individual identification for behavioral research: "At first the metal ring seemed merely to be a new aid to migration research. But then the marking of individuals proved to have a much more comprehensive significance, because it helped the study of behavior on the breeding grounds..." (Stresemann 1975: 338). By the 1930s, "further important insights into the structure and dynamics of societies were provided by the colored band, by which an individual bird can be recognized without being caught... For the first time it was possible to follow the fate of individual birds from birth to death, determine exactly their fertility rate, examine their relation to other members of the same population, and obtain much other information about which previously there has been only the vaguest notions" (Stresemann 1975: 359).

In animal behavior, the individual became the unit of theoretical interest because

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[9] Rubenstein and Wrangham 1986: 4

of the "growing acceptance of the evidence that the potency of natural selection is overwhelmingly concentrated at levels no higher than that of the individual" (Alexander 1974: 325). As a result, "in the past twenty years... there has been a theoretical revolution in evolutionary biology, leading to reexamination of early work... and a dramatic increase in studies designed to clarify how factors such as kinship, reciprocity, sexual selection and life history affect the evolution of behavior" (Cheney *et al.* 1987: 2). Following the principles of maximizing individual reproductive success (Williams 1966) and kin selection (Hamilton 1964), "animals came to be viewed as individuals who were armed with many behavioral options in their struggle for maximizing either their own reproduction, or that of their relatives... By analyzing the behavior of individuals, the foundations for a comprehensive theory of social behavior were laid" (Rubenstein and Wrangham 1986: 4). From this theoretical perspective, animal behavior studies came to emphasize long-term monitoring of known individuals to assess factors that influence lifetime reproductive success.

From a methodological point of view, focusing on the behavior of one individual at a time, *i.e.*, focal-animal sampling (Altmann 1974), is the principal means of minimizing the intrinsic biases in observational studies. "Asked to prepare a short piece on different ways of analyzing [behavioral] data, [Jeanne Altmann] ...decided the problem was not really how people analyzed data... The problem was how people *collected* data... The embarrassing truth was that many of the regularly cited field studies especially before the mid-1970s both gathered and analyzed data in a way that did not justify the conclusions reached" (Haraway 1989: 307). Altmann (1974: 229) suspected "that the investigator often chooses a sampling procedure without being aware that he is making a choice." To make the choices explicit, Altmann (1974) wrote what has come to be regarded as the preeminent handbook for behavioral sampling methods.

Following Altmann (1974) and others, focal-animal sampling in studies of terrestrial animals routinely takes the form of following a known individual for a

specified length of time while recording selected behavioral information in a systematic fashion. These "follows" are repeated over periods of weeks, months or years. In comparison with the snapshot, cross-sectional viewpoint provided by census methodologies, protracted follows furnish a more comprehensive, longitudinal perspective of social phenomena, encompassing not only the flashy acts likely to catch an observer's eye but also quiet intervals that can be equally revealing about an animal's social life. From standard census methods, information about group composition and preferred associates within groups can be derived; protracted follows, however, are integral to an appreciation of the competitive or cooperative nature of social relationships.

Attention to the social relationships of primates brought further conceptual advances in animal behavior. In particular, "...the new thing that students of primate behavior did was to recognise the individuality of their animals..." (Rowell 1994). By the 1980s, "...groups of individually recognized [primates] have been studied continuously for 10 years or more... [These] long-term primate studies were among the first to show the critical importance in mammals of kinship, social relationships, and individual variations in behavior" (Smuts *et al.* 1987: ix). In particular,

> "...widespread existence of long-term social relationships among primates has frequently forced primatologists to approach the evolution of behavior with a [different] perspective... [T]raditional ethological research has concentrated on interactions between individuals and has examined the function of single acts by measuring their immediate and long-term consequences. In primates, however, an interaction like grooming clearly has consequences beyond both its immediate function of ectoparasite removal and the longer-term function of making subsequent grooming bouts more likely, since grooming can also contribute to the maintenance of a relationship that may have important reproductive consequences... [Thus] primate studies have begun to document the importance of analyzing behavior at the level of social relationships..." (Cheney *et al.* 1987: 4).

These advances in the field of animal behavior have yet to be integrated into studies of cetacean social behavior. By and large, research on the social behavior of whales and dolphins has scarcely advanced beyond Saayman's records of "whatever one

can see..." (see Norris 1991*a*, above). For example, even though recognition of individual animals is now common practice both in studies of animal behavior and in cetacean field studies, the union of the two conditions has yet to be accomplished: *i.e.*, individual recognition is by no means commonplace in studies of the social behavior of cetaceans. The shift in focus from blue whale units and whaling stocks to individual whales and dolphins has only tangentially been applied to obtaining a better understanding of the social behavior of individual cetaceans. Instead, each uniquely-distinctive cetacean has primarily contributed to population-level statistics; each individual whale and dolphin is first and foremost a necessary cipher in the mark-recapture equations utilized to assess population well-being.

This observation is not intended to minimize the essential nature of the conservation-based endeavor. Rather, the intent is to highlight the irony in that, having borrowed a tool from behavioral research -- individual recognition *via* natural markings -- cetologists have yet to embrace application of this device to its original purpose -- behavioral research. Although some cetacean biologists acknowledge that the ability to identify individuals could "lay the foundation for modern behavioral studies of ...whales" (*e.g.*, Payne *et al.* 1983: 373), it is rare that field studies of social behavior have actually focused on individual whales and dolphins (but see, *e.g.*, Pryor and Kang 1980; Taber and Thomas 1982; Thomas and Taber 1984; Connor *et al.* 1992; Smolker *et al.* 1993; Sayigh *et al.* 1995). It is paradoxical that the IWC Special Report entitled *Individual Recognition of Cetaceans* (IWC 1990) was wholly dedicated to the importance of individual identification for estimating population parameters, while the significance of individual recognition for understanding social behavior merited no more than obscure mention (*e.g.*, Würsig and Jefferson 1990).

Instead of concentrating on individuals, behavioral information about cetaceans is typically the product of group-focused *ad libitum* sampling recorded during census efforts or chance encounters (Mann and Tyack, in press). Altmann (1974: 235) defined

ad lib. sampling as "typical field notes... often with the observer recording 'as much as he can' or whatever is most readily observed of the social behavior of a group in which the behaviors, individuals and often the times for behavior sessions are chosen on an *ad libitum* basis." Altmann (1974: 236) was explicit about the drawbacks of data collected in this manner:

> "With *Ad Lib.* sampling, it is rarely possible to determine which differences in data are due to true differences between individuals, age-sex classes, or behaviors, and which due merely to biases in sampling. When comparing the results of one such study with those of another, we cannot tell which differences were due to differences in what could be seen, which to differences in what was selected for recording, and which to actual differences in the populations."

Much of what cetologists label as "group-focal" observations is essentially *ad lib.* sampling of conspicuous behavior (Mann and Tyack, in press). This is because true group-focal sampling is acceptable only under rarely-met circumstances: "[Sampling] of a focal (sub)group of several animals... will usually be practicable only when it is possible to keep every member of the focal subgroup under continuous observation during the sample period" (Altmann 1974: 243). This strict requirement is seldom achieved in observations of social groups of any animals, much less in observing ephemeral groupings of cetaceans. Even attempts to systematize so-called group-focal observations cannot overcome the inherent sampling dilemmas that result when all group members are neither equally visible nor equally engaged in the same activity. Thus, although group-focused observations can provide beneficial information (*e.g.*, primates: Bernstein 1991; cetaceans: Shane 1990; Slooten 1994), attention to one individual at a time is the procedure of choice when the goal is to obtain reliable estimates of frequencies, rates, sequences, or durations of behavior (Altmann 1974).

In addition to ignoring the perspective of the individual animal, methodologies for studying cetacean social behavior have rarely incorporated protracted follows. It was long believed that follows were impossible to achieve at sea (*e.g.*, Ohsumi 1971) or disruptive to the animals' behavior (*e.g.*, Würsig and Würsig 1980). While these barriers may exist

in studies of some species at certain locations, there are now several examples in which focal-animal sampling has been successfully adapted to study the social behavior of cetaceans (see below). In particular, the problem of habituation to observers (and their vessels), a key component of behavioral research, has too often been approached by cetologists as an all-or-nothing proposition, rather than a connection that must be earned. After all, it took eight months before the chimpanzees stopped running away from Jane Goodall, and another ten months before they permitted sufficiently close approaches that she could observe social behavior (Goodall 1986)!

Despite unambiguous discourse in the behavioral literature regarding the inadequacies of group-focal and *ad lib.* sampling for documenting social behavior, these techniques are so ingrained in cetacean biology that, in a 1994 European Cetacean Society guide to field methods, so-called group-focal sampling was presented as *de rigueur* for studies of bottlenose dolphins (Politi 1994, following Shane 1990). The uncritical endorsement is perplexing. In a discipline that has gone to extensive lengths to ensure the precision of population-level appraisals (*e.g.*, Hammond 1986; IWC 1990), it is ironic that no comparable degree of rigor has been applied to field studies of social behavior. Why is this the case?

"The 'soft' fringe of biology" [10]

> *"Photography is usually not compatible with behavioral observations, being time consuming and so demanding of attention that considerable information may be lost."* George B. Schaller 1965: 628

The conservation-based focus of cetology has resulted in several conflicts of

[10] Gaskin 1982: 112

interest -- both presumed and actual -- between obtaining population-level statistics and monitoring the social behavior of individual cetaceans. The seriousness of the conservation task, the conventional methods used to achieve population parameters, the management-focused funding opportunities, and the misperception that behavioral biology is neither "serious science", nor integral to conservation efforts, have all conspired to relegate studies of cetacean social behavior to a back seat.

If knowledge about social behavior were perceived to be a key element in cetacean conservation endeavors, this would not be an issue. But despite the saga of the sperm whale mating system, social behavioral issues have generated limited regard, and therefore, flaws in the methodological and conceptual approaches to studying cetacean social behavior have received little scrutiny. In part, this lack of consideration stems from a belief that behavioral research is "soft science", a viewpoint not restricted to cetology: "The spurious view that much basic behavioural research is of no practical use -- and therefore a waste of time -- is more prevalent than in the case of, say, physiological or biochemical research. This is at least partly because people have insight into their own actions and may also be familiar with the behaviour of some animals" (Martin and Bateson 1994: 2). Indeed, even some fellow biologists look down on behavioral research as non-quantitative pseudo-science. Gaskin (1982: 112) probably expressed the frustration of many by saying:

> "No research on Cetacea has attracted more public attention in recent years than work on their behaviour, communication and intelligence... Yet surely no aspects are more difficult for the scientist to study effectively. The biologist, educated to respect the 'hard data' of the numbers and weights of population samples or the calculated values from studies of cellular enzymatic reactions and blood chemistry, usually views behavioural work as occupying the 'soft' fringe of biology (meaning that area which abuts on psychology, and is therefore barely respectable)."

Norris (1991*c*: 218), a behaviorist himself, had worries about internal validity: "Behaviorists especially... have had to struggle to escape viewpoints based on their own lives rather than the lives and environment of the animals under observation." The

friction between behavioral and population biologists was exemplified in the report of a 1982 workshop on behavioral issues in whale management (IWC 1986: iii): "Prior to that meeting cetologists studying behaviour and cetologists studying population dynamics had kept themselves to themselves, apart from the occasional complaint from the behavioural people that modellers took no account of their work and the riposte from the modellers that until the behavioural observations were quantified it was impossible to incorporate them into models."

All of the above-named concerns were precisely what Altmann (1974) had set out to resolve. She proposed that judicious use of "sampling decisions ...in observational studies of social groups can increase the validity of comparisons both within and between studies, whether observational or experimental, field or laboratory" (Altmann 1974: 231), thus countering the claim that "quantitative research on behavior is not practicable in the context of ongoing, real-life situations" (Altmann 1974: 229). Judicious use of sampling decisions has been all too rare in research on cetacean social behavior, and these qualitative, *ad lib*. studies have consequently been viewed with skepticism.

This skepticism has had repercussions with respect to financial support. Basic (non-applied) research on cetacean social behavior tends not to come under the purveyance of conventional funding sources for marine mammal research that are focused on management issues or sensory systems. Nor are studies of cetacean social behavior often acceptable to traditional funding sources for animal behavior because they are rarely considered state of the art. This opinion was succinctly expressed by the National Science Foundation's Animal Behavior Panel (1992) in an otherwise favorable review of a grant application: "Unfortunately... cetacean [behavioral] research in general has suffered from a lack of focus and methodological rigor." As a consequence, cetologists seeking funding for social behavioral research fit into few of the available funding slots unless projects can be repackaged with a management emphasis.

Can studies of cetacean social behavior be raised to a level of rigor that would be acceptable to animal behavior funding sources? Can research on cetacean social behavior be reconciled with the exclusive population biology emphasis in cetology? Methodologically, cetology is wed to obtaining estimates of population and life history parameters using mark-recapture models. The preferred methods for population- *versus* individual-level studies -- photo-identification and censusing *versus* protracted follows -- are generally regarded as incompatible: "Ongoing studies involving photo-identification have a variety of objectives and some, such as behavioural investigations emphasizing focal animals, require sampling strategies that are not ideal for providing data useful in estimating population size" (IWC 1990: 7).

It is true that protracted follows of known individuals, the preferred mode for monitoring social relationships, are unlikely to generate population-level data as rapidly as census-and-move-on efforts. Protracted follows, however, are readily combined with other protocols, and in fact, are most effective when integrated with broader information-gathering schemes. For example, in studies of primates, focal-animal sampling is typically combined with systematic records of group composition and preferred associates, assessments of female reproductive status or infant developmental stages, and ecological factors as well as *ad lib.* behavioral records (*e.g.*, Altmann 1980; Smuts 1985). Thus, the desirable merger of population- and individual-level data collection procedures may well be feasible, at least in long-term cetacean field studies where many individuals are frequently encountered and readily recognized.

Harder to reconcile with studies of social behavior is the cetologist's pre-occupation with "shooting whales (photographically) from small boats" (Mizroch and Bigg 1990: 39). "Photo-identification of naturally marked cetaceans helps obtain information on group structure, site fidelity, movement patterns and population size... [and] can also enhance descriptions of life history parameters such as age at sexual maturity, calving intervals and reproductive and total life span... [R]efinement and

increasing sophistication [of the photo-identification technique] ...promise to make it increasingly important in life history and social systems studies of small cetaceans" (Würsig and Jefferson 1990: 43). On the down side, the emphasis on data collection through the viewfinder of a camera has severely impaired research on cetacean social behavior. Some of the drawbacks were vividly portrayed by True (1903: 92), an early photographer of fin whales: "[T]he difficulty of getting the picture itself is so great that one's faculties are entirely absorbed in the proceeding and there is little opportunity for observing particulars. The pitching and rolling of the steamer in the restless waters is very disconcerting, and not less so the fact that the point at which the whale will appear is uncertain and the length of time it will remain in view very brief." Even though the technology is much improved since True's day, it is still the case that a primary emphasis on photography is incompatible with systematic collection of social behavior data.

As Schaller, True, and others have pointed out, the camera's lens is a narrow perspective from which to observe and interpret the complexities of social behavior among gregarious animals. Because individual recognition of cetaceans has become synonymous with photo-identification (*e.g.*, IWC 1990), animals encountered at sea often go unrecognized until the contact sheets come back from the photo lab, and therefore, identities of socializing partners may be irretrievable. To compensate, extensive effort has gone into deriving the maximum amount of information from photographs of cetaceans, and cetologists have come to believe that photographic techniques actually provide more reliable findings.

Consider, however, the extreme example of this kind of analysis in which strong social bonds are determined to exist for individuals only if they are repeatedly photographed in the same frame (*e.g.*, Würsig 1978; Heimlich-Boran 1986). How much information may be lost because some social associates seldom surface in synchrony (and therefore rarely have their picture taken together); how much is missed because of the difficulties in obtaining multiple, in-focus fins in a single shot? Moreover, as Bigg *et al.*

(1990: 387) noted: "[W]hales in a frame were not necessarily equally associated. In a frame containing three individuals, two may have been in close proximity to one another with a third off in the distance."

Using a less artificial measure -- *i.e.*, "individuals that consistently surfaced within 1-2 body lengths... of each other were considered to be the most strongly bonded" -- Bigg *et al.* (1990: 386) concluded that "association analysis [from photographs of killer whales] was more useful for quantifying the strength of bonds and for establishing subtle bonds that could not be detected by direct observation." However, the inadequacies of real-time observation may have had much to do with employment of *ad lib.* sampling methods. In contrast, studies of terrestrial mammals have demonstrated that social bonds are readily and accurately obtained from direct observations *when* judicious use of sampling decisions is exercised, *i.e.*, when data are collected in a systematic, quantifiable manner (*e.g.*, Altmann 1980; Smuts 1985; or any recent study of primate social behavior).

Granted, it is sometimes true that "...photographs show a number of details not noted at the time they were taken" (True 1903: 92), and the markings of some cetacean species may not be amenable to on-the-spot recognition. However, the more prevalent objection to direct observations is that "real-time identifications 'by eye' alone do not provide the degree of certainty about identifications that is necessary for [population-level] analyses..." (Wells and Scott 1990: 412-3). Wells and Scott (1990: 412-3) tested their "ability to identify by eye the resident Sarasota dolphins... by examining a sample of 48 schools observed during 1986 and 1987 for which ...all identifiable dolphins were captured in the photo record... On average, 89.3%... of the dolphins present were correctly identified in real time." Concluding that nearly 90% accuracy was unacceptable, they rejected real-time identification.

Elephant researcher Ian Douglas-Hamilton began with a similar point of view.

Because "many elephants looked similar to others and were distinguishable only by minute differences, ...I therefore believed that photography was probably the only method of recording details with sufficient accuracy"; however, when he decided to conduct follows of individual elephants, a colleague insisted that he make sketches rather than rely on photographs because "the problem of making notes while taking photographs would inevitably lead to greater muddles" than the occasional misidentification (Douglas-Hamilton and Douglas-Hamilton 1975: 43). Douglas-Hamilton soon learned to recognize many individual elephants by eye, while continuing to maintain a catalog of photographs for confirmation.

Douglas-Hamilton's experience suggests that the results of Wells and Scott (1990) may, in fact, be good news for the prospects of direct observations. Wells and Scott (1990) viewed each dolphin school for an average of 19.3 minutes during censusing efforts. This begs the question: would longer stays with dolphins, and in particular, repeated, protracted follows of certain individuals and their associates, achieve higher levels of accuracy? In addition, the Sarasota results indicated that, as with killer whales, "most individuals were recognizable by eye, but some required a good photo for positive identification" (Bigg *et al.* 1990: 385). This begs the further question: mightn't Douglas-Hamilton's compromise solution be relevant here? If readily-recognized animals can be accurately identified by eye, the photographic workload can be reduced to the unfamiliar or faintly-marked few, thus freeing up substantial time for observing social behavior.

These questions are not rhetorical; in fact, positive returns are already in. A descendant of the semisubmersible seasick machine enabled Östman (1994; Norris and Wells 1994) to conduct focal follows of spinner dolphins and monitor nearly all occurrences of a focal's social interactions (*i.e.*, continuous behavioral sampling: Altmann 1974); these follows, however, were brief, lasting tens of minutes at best. More prolonged follows of cetaceans have typically been conducted from above-water, resulting in interruptions of surface observations of social behavior when animals go underwater

and out of sight. Nevertheless, even without assurance that all occurrences of behavioral interactions can be recorded, such protracted follows of individuals have led to significant advances in understanding, for example, the developmental stages of right whale calves (Taber and Thomas 1982; Thomas and Taber 1984).

In addition, in Western Australia, collaborative, long-term studies of bottlenose dolphin social behavior, modelled on primate field research, have shown that focal-animal sampling can be effectively combined with photo-identification and censusing efforts to provide detailed information of interest to behavioral biologists (*e.g.*, the whistles and behavior of bottlenose dolphin mothers and calves: Smolker *et al.* 1993; Mann and Smuts, in press; and the alliances among male dolphins: Connor *et al.* 1992) as well as population biologists (*e.g.*, social structure and association patterns: Smolker *et al.* 1992; female reproduction: Richards 1994). In Sarasota as well, focal-animal sampling projects now co-exist alongside community-level investigations (Wells 1991). For example, focal follows of bottlenose dolphin calves have been used to identify social factors that influence signature whistle development (Sayigh *et al.* 1995).

Protracted follows of sperm whale groups have also been crucial in clarifying their social structure and revealing, at long last, their mating system. Whitehead and Gordon (1986: 155) "described [an acoustic tracking] method whereby schools of females can be followed for a week or so, and a single whale for a day or two, while behavioural interactions are observed. We believe that this methodology is the key to answering the important questions about sperm whale behaviour." They felt that lengthy follows were necessary for studying these deep-diving whales because "most observations were of sub-groupings of a larger school, whose members were never all seen together at the surface at the same time" (J. Gordon 1987: 214). They found that protracted follows furnished additional detail about associations among females: "The general pattern ...is that female sperm whales and their offspring possess two types of associates: some who stay associated for about 4-20 days, and others who are constant companions for a year or

more... It is quite possible that these stable associations... are 'family units',... [*i.e.*,] closely related females, plus male offspring younger than the age of dispersal..." (Whitehead *et al.* 1991: 386-8).

With respect to the sperm whale mating system, it has been of long-standing concern that "...despite the examination of hundreds of thousands of carcasses ...interactions between mature males and schools principally composed of mature females are poorly understood, and have great bearing on the resultant population dynamics..." (Whitehead & Gordon 1986: 149). Whitehead and Gordon (1986: 156) believed that "if we can conduct watches of groups of females lasting five days or more, at times when large males are with them for the purpose of mating, then we can learn a considerable amount about the mating system of the sperm whale." Their prediction proved true:

> "Whitehead and Arnbom (1987) found that individually identified male sperm whales associated with a variety of groups of females and *vice versa*. The average duration of an interaction between a male and a group of females was only a few hours... This implies that males are moving between groups of females searching for oestrous females rather than holding harems... Changing the sperm whale model to incorporate a 'searching' male mating strategy suggests that the female pregnancy rate is more resilient to relative male depletion than in the traditional 'harem' model..." (Whitehead 1990: 377-8).

THE STAGE IS SET

It seems clear from these examples that despite the difficulty and the cultural factors, sophisticated studies of cetacean social behavior can now be accomplished, at least in long-term field studies of coastal cetaceans where focal individuals can recognized by eye and located for sampling on a regular basis. The difficulty factor has been vanquished several times over: as a result of hard work, perseverance, and the development of ingenious technologies, it is now possible to recognize individual cetaceans within the context of demographic factors, familial relationships, and social

associates. It is time to overcome the cultural factors: to recognize that social behavioral research is "hard science", to learn the techniques of systematic behavioral sampling, to appreciate the contributions of complementary captive and field studies, and to acknowledge the significance of social relationships. The stage is set to embark on focused, quantitative studies of the social behavior of cetaceans.

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CHAPTER 2. A QUANTITATIVE ASSESSMENT OF DOMINANCE RELATIONS AMONG BOTTLENOSE DOLPHINS

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ABSTRACT

Agonistic behavior of bottlenose dolphins was studied at Brookfield Zoo for nearly 4.5 yr, and dominance relationships were determined using a quantitative technique adapted from primate behavioral research. Dominance relations among dolphins were influenced by the gender of participants. Male dolphins were clearly and consistently dominant to females, and intersexual agonism occurred at moderate rates with seasonal peaks in spring and fall. Dominance relationships among female dolphins were age-ordered and stable, even though agonism among females did occur at uniformly low rates. In contrast, the two males had a changeable dominance relationship in which periods of stability and low-level agonism were interspersed with episodes of intense competition. Zoo-based research revealed patterns of behavior that conformed to current knowledge about bottlenose dolphin social structure. Moreover, research in a zoo setting facilitated development of a quantitative technique that can be used to assess cetacean dominance relationships in field research.

INTRODUCTION

Competition for scarce resources is often expressed among group-living mammals in agonistic dominance relationships. Social dominance is such a prevalent feature of terrestrial mammalian societies that noteworthy species are ones for which dominance is absent (*e.g.*, African lions: Packer *et al.* 1988). The concept of social dominance and its measurement have been debated extensively (reviewed in Bernstein 1981). However, there is general agreement that, when dominance is defined by the directionality of

aggressive-submissive or approach-retreat encounters between pairs of individuals (*e.g.*, Rowell 1966; Hausfater 1975), dominance relationships can be highly consistent over time (reviewed in Walters and Seyfarth 1987). Such long-term dominance relations can explain much of the variation in reproductive success and access to resources (reviewed in Dewsbury 1982; Harcourt 1987; Silk 1987). Moreover, benefits conferred by high social status may be lifelong (*e.g.*, olive baboons: Packer *et al.* 1995).

For many mammals, dominance relationships correspond to physical attributes related to competitive ability such as male body size (olive baboons: Packer 1979; red deer: Clutton-Brock *et al.* 1982; elephant seals: Le Boeuf and Reiter 1988) or female age (red deer: Clutton-Brock *et al.* 1982; American bison: Rutberg 1983). Among highly-social species with long-term relationships between individuals, dominance relations may be associated with individually-specific factors and rely on individual recognition. For example, dominance relations among females in matrilineal societies are associated with social factors such as kinship (*e.g.*, bonnet macaques: Silk *et al.* 1981; savannah baboons: Hausfater *et al.* 1982; spotted hyaenas: Frank 1986).

The patterns of competitive behavior usually differ between the sexes within a species (*e.g.*, Clutton-Brock *et al.* 1982), ultimately corresponding to differences in the resources for which males and females compete. Typically females compete for access to resources necessary for reproduction, whereas males compete for access to females (Trivers 1972). As a result, competition among females tends to be constant and low level because advantages to females accrue slowly over time; in contrast, competition among males can be intense and episodic because benefits to males may be large and transitory (Smuts 1987).

Most cetaceans are group-living and many odontocetes, in particular, live in structured social groups characterized by long-term associations between individuals (reviewed in Tyack 1986). For example, longitudinal studies of bottlenose dolphins

(*Tursiops* spp.) reveal complex patterns of long-term relationships (Wells *et al.* 1987; Wells 1991; Connor *et al.* 1992; Smolker *et al.* 1992). Adult males form stable bonds with one or two other males that persist for many years, and relationships tend to be cooperative within a male's unit and antagonistic with some other male units. Adult females associate over a broader network of individuals but also have close, long-term relationships with specific females including matrilineal kin. Social dominance and sex differences in competitive behavior might be expected as features of such a society in which individuals have long-term relationships based on gender and individual recognition.

Although no field studies have focused on cetacean dominance relationships, conspicuous dominance hierarchies have been described for captive social groups of delphinids (McBride 1940; McBride and Hebb 1948; Essapian 1953, 1963; Tavolga and Essapian 1957; Tavolga 1966; Caldwell and Caldwell 1972; Tayler and Saayman 1972; Bateson 1974; Östman 1991) and beluga whales (Recchia 1994). These accounts provide valuable insight into cetacean sociality, but few assessments have been quantitative (but see Bateson 1974; Östman 1991; Recchia 1994). In the present study, we introduce a quantitative technique for assessing dominance relations among dolphins, adapted from methods used in studies of baboons (Hausfater 1975; Hausfater *et al.* 1982). We describe longitudinal patterns of dominance relations based on quantitative behavioral data and evaluate these patterns in the context of bottlenose dolphin social structure.

METHODS

Dolphin Colony

The Brookfield Zoo (BZ) colony of Atlantic bottlenose dolphins (*Tursiops truncatus*) consisted of two males and five females during the study period, January 1988 through May 1992 (Table 1). Two males (Nemo and Stormy) and one female (Windy) were colony members throughout the study. Four resident social groups were defined corresponding to long-term changes in colony membership (Table 2). In addition, two

females from Minnesota Zoo were housed temporarily in an adjacent pool and introduced to resident females during 16 days in January 1990 (Table 1).

Maturational classification of females was based on known reproductive status or age (Table 1). We considered each female to be reproductively mature (adult) at the time of her first conception; we also included as adult two older, nulliparous females (estimated ages 30+ and 15+ yr). Two younger, nulliparous females (11-13 yr) were classified as "maturing," and a young, clearly prereproductive female (4-5 yr) as "juvenile."

We were unable to define the maturational status of BZ males as precisely as for females. Based on age (Table 1), both were past onset of sexual maturation, *i.e.*, "maturing" (Wells *et al.* 1987). However, in absence of hormonal or paternity data, we could not determine whether only one or both males had achieved adulthood, *i.e.*, had begun to sire offspring. An age criterion was not appropriate because first reproduction is reported to occur over a wide range of ages: for example, wild males in Sarasota FL typically do not sire offspring until > 20 yr of age (R. Wells, personal communication), whereas at least one male in captivity sired offspring as young as estimated age 8 yr (J. Sweeney, personal communication). Because each BZ male could not be exactly classified, we designated both as "adult/maturing." Growth patterns (Table 3) suggested that older, full-grown Nemo was more mature than still-growing Stormy.

The dolphins lived in a complex consisting of four interconnected pools: an oblong main pool (33.5 x 12.2 x 7.6 m), two circular holding pools (10.7 m diameter x 4.3 m deep), and a circular medical pool (7.6 x 2.4 m). During October 1988-May 1989, dolphins lived temporarily in a single pool (30.5 x 7.6 x 4.9 m).

Behavioral Sampling

Dominance assessment was one component of long-term research on social

relations among BZ dolphins. Behavioral sampling was based on a focal-animal sampling scheme (Altmann 1974) in which the activities, associates, and social interactions of a single dolphin were the focus of each observation session. In 1988, only males were focal subjects of 20-min observation sessions; in 1989-1992, all dolphins were focal subjects of 10-min sessions. Several focal subjects were chosen each observation day using a predetermined, randomized schedule to promote equal, unbiased sampling of all individuals.

Year-round observations were conducted near-daily between 0700-0900 before onset of the dolphins' daily scheduled activities with humans. Dolphins were habituated to the presence of observers who did not feed or interact with them during observation periods. At the multipool facility, observations were typically conducted through large, underwater windows that afforded close-up viewing of entire behavioral sequences; at the single-pool facility, observations were conducted from a vantage point of 6-7 m above water. Observers were experienced in dolphin care, training, and/or behavioral research; underwent months of training in data collection techniques; and routinely worked in pairs to ensure consistency of data.

We used a continuous sampling scheme (Altmann 1974) in which we recorded all occurrences of the focal dolphin's involvement in specified social interactions, including agonistic interactions analyzed herein (Table 4). In addition, we opportunistically recorded social interactions of non-focal dolphins, *i.e.*, *ad libitum* sampling (Altmann 1974). We defined a social interaction to occur when dolphins were within 1 m of each other and one dolphin directed one or more specified behavior(s) toward another. The 1-m criterion was based on preferential association patterns that were discernable at one, but not two, meters (Samuels, unpublished data). Onset of a new interaction was signified by a change in partners or a break of $>$ 10 sec in the sequence of behaviors. Each record of a social interaction included a list of all behaviors performed and identities of actors and recipients, annotated to indicate which behavior was performed

by which partner. Behavioral data were dictated into a hand-held cassette recorder and later transcribed onto checksheets using a standardized coding scheme.

DATA ANALYSES

Identifying Dominance Interactions

Agonistic interactions that contained one or more specified aggressive and/or submissive components (Table 4) were extracted from the larger dataset of all focal and *ad lib.* social interactions. The aggressive and submissive behaviors included those that were generally agreed to be expressions of agonism for delphinids (references listed in Table 4) and other mammals (*e.g.*, baboons: Hausfater 1975). In general, aggression was typified by threats and forceful attempts to inflict harm, while submission was typified by behaviors associated with avoidance, withdrawal, and escape. In this study we identified for the first time for cetaceans, the submissive behavior "flinch" (Table 4), which is the cetacean equivalent of a primate "cower" (*e.g.*, Hausfater 1975). Aggressive behaviors included "pin" (Table 4), a behavior traditionally described in the context of mother-calf interactions (*e.g.*, Tavolga and Essapian 1957) but which we observed in interactions between males.

A total of 2,230 dyadic agonistic interactions (focal and *ad lib.*) were recorded during approximately 681 h of observation during the 53-month study. Interactions observed during the first two weeks of introductions, between dolphins held in separate pools, or involving mothers of neonates were not included in analyses unless specifically indicated. Behavioral data were entered into a relational database program (Paradox 1992); results were plotted using computerized graphics (Axum 1992).

Evaluating the Outcome of Dominance Interactions

Assessment of dominance relations was based on focal and *ad lib.* data. Inclusion of *ad lib.* data is appropriate in evaluating the direction and degree of one-sidedness in relations between pairs of individuals (Altmann 1974). Outcomes of agonistic

interactions were determined using explicit rules developed to evaluate long-term dominance relationships among baboons (*e.g.*, Hausfater *et al.* 1982; Samuels *et al.* 1987). Following Hausfater (1975), the dominance assessment was based on agonistic interactions that (1) involved a pair of dolphins and (2) had a clearly decided outcome. Polyadic interactions were not considered in this report. Decided agonistic interactions were those in which one individual (the "loser") performed submissive behaviors and no aggressive behaviors, in response to non-submissive behaviors by the "winner" (Table 5). Behaviors performed by the winner could be aggressive or neutral (*i.e.*, non-agonistic). Thus, outcomes of decided agonistic interactions were determined by the ability of one dolphin, by means of aggression or otherwise, to force an opponent to behave submissively, *i.e.*, to "back down."

This dominance assessment technique, based on outcomes of agonistic encounters, differed from schemes based solely on aggression used in previous studies of delphinids (Bateson 1974; Östman 1991). Use of submissive criteria to assess dominance relations upheld a long tradition in primate behavioral research, following the assertion by Rowell (1966) that lower-ranking individuals were the ones who perpetuated rank distinctions by their subordinate actions.

In agonistic interactions that did not conform to the above-stated model for decided interactions, neither opponent could be designated as a winner. Consequently, these undecided interactions were not used in assessment of dominance relationships. Predominant forms of undecided agonism were listed in Table 5.

Assessing Dominance Relationships

Dyadic dominance relationships were determined by compiling decided agonistic interactions for each pair. A dolphin was identified as dominant member of a pair during months in which that individual won a preponderance (*i.e.*, 76%-100%) of decided interactions with the opponent. During months in which few agonistic interactions

occurred, we assumed persistence of the preceding relationship because established dominance relations were likely to reduce the tendency to engage in competitive conflicts (*e.g.*, Bernstein 1981). Periods of unstable relations were defined to occur when neither partner won a clear majority of interactions and thus neither could be identified as dominant member of the pair.

For assessments involving relationships of several individuals, we constructed dominance matrices (contingency tables) in which winners and losers were represented in rows and columns, respectively, and cell entries contained the frequency of corresponding dyadic interactions (Altmann 1974). Winners were ordered so as to minimize the percentage of entries to the left of the matrix diagonal, *i.e.*, reversals or encounters won by a typically subordinate individual.

Rates of Agonism

Rates of agonism were calculated using focal data only; use of *ad lib.* data is not appropriate for analyses of frequency (Altmann 1974). Agonism rates (*i.e.*, number of agonistic interactions per min) were calculated per focal dolphin per month of the study per partner type (*i.e.*, male *vs.* male; female *vs.* female; male *vs.* female). Each rate calculation was adjusted by the number of partners available per partner type for each month of the study. For comparisons among adult and maturing dolphins, this partitioning resulted in 350 rate calculations based on 1,266 focal agonistic interactions.

Rates of agonism were compared by partner type for adult and maturing dolphins. Inspection of the data suggested that sample variances were unequal; however, we chose not to homogenize variances by data transformation because we were interested in variability of agonism rates by partner type. Instead, to test for homogeneity of sample variances, we used Hartley's F_{max}-test (Sokal and Rohlf 1981). To compare agonism rates by partner type, we used the Games and Howell method for testing equality of means when variances were heterogeneous, an alternative to analysis of variance in cases of

unequal sample variances (Sokal and Rohlf 1981).

Because some *Tursiops* populations exhibit reproductive seasonality (in captivity: Urian *et al.* 1996; in the wild: *e.g.*, Wells *et al.* 1987), we looked for seasonal patterns in median monthly agonism rates of adult and maturing dolphins partitioned by partner type. We excluded time periods in which seasonal reproductive patterns were likely to have been obscured by other factors: January-February 1989 (separation and re-introduction of males); 1991 (addition of new females who conceived within two months of introduction regardless of season); 1992 (only 5 months of data)). In addition, rates of female *vs.* female agonism could not be compared on an annual basis because no females were focal subjects in 1988, and only a single female was present in 1990. Therefore, only male *vs.* male and male *vs.* female agonism could be evaluated for seasonality. Because two months were excluded from the 1989 sample, statistical comparison was restricted to data from 1988 and 1990.

Agonism involving the sole juvenile was analyzed separately from that of adult and maturing dolphins because social conventions for mature animals may not strictly apply to prepubescent individuals (*e.g.*, primates: Pereira and Altmann 1985). Monthly agonism rates were calculated for the interactions of each of five focal adults with the juvenile female during November 1991-March 1992 (a five-month period when there were no temporary perturbations in group composition). The resultant 25 rate calculations were based on 58 focal agonistic interactions involving the juvenile.

Non-parametric tests were used to compare agonism rates: *e.g.*, each male's rate of agonism with females; each adult's rate of agonism with a juvenile female *vs.* with adult females; male *vs.* male rates during different periods; seasonal patterns by year.

RESULTS

Sex-related Differences in Rates of Agonism

Among adult and maturing dolphins, males were involved in the highest rates of agonism, and rates of male *vs.* male agonism were most variable. In contrast, females engaged in agonism with each other at rates that were uniformly low. Specifically, agonism between males (MM) occurred on average once per 38 min (mean rate = 0.026 interactions per min); between males and females (MF), once per 45 min (mean rate = 0.022); and between females (FF), once per 167 min (mean rate = 0.006) (Fig. 1). Rates of agonism between females (FF) significantly differed from those involving males (MM, MF) (Games and Howell test of equality of means (Sokal and Rohlf 1981): $MSD_{FF,MM} = 0.015$, $P < 0.05$; $MSD_{FF,MF} = 0.009$, $P < 0.05$); whereas MM and MF agonism rates were not different from each other ($MSD_{MM,MF} = 0.015$, ns).

Rates of male *vs.* male agonism were also more variable (MM variance = 0.0018) than agonism of other partner types (MF variance = 0.0007, FF variance = 0.0002). Variances per partner type were significantly heterogeneous (Hartley's F_{max}-test for homogeneity of variances (Sokal and Rohlf 1981): $F_{max} = 2.2$, $P < 0.01$). For all partner types, there were months of no agonism; males additionally experienced periods of intense competition with each other, with mean monthly agonism rates ranging as high as 0.2 interactions per min (*i.e.*, once per 5 min).

In addition to partner gender, agonism rates may also have been influenced by partner age in the sense that juvenile behavior may differ from that of older dolphins. For each adult in Group 4, we compared the rate of agonism with adult females *vs.* with the juvenile female during a five-month period. Monthly agonism rates of three adult females were significantly higher when their partner was a juvenile female (mean rate = 0.018 interactions per min) than when both partners were adult females (mean rate = 0.002) (Wilcoxon matched-pairs signed-rank test, $T = 0$, $P < 0.02$, $n = 7$ comparisons in which monthly rate > 0). Although agonism rates of the two males were similarly

higher when their female partner was a juvenile (mean rate = 0.028) *vs.* adult (mean rate = 0.010), the difference was not significant (T = 13, N.S., n = 8). Based on agonism involving a single juvenile, however, we could not determine whether these differences were due to her young age or individual variation.

Dominance Relationships

Due to sex differences in variability and rate of agonism, we evaluated the dolphins' dominance relationships within partner types that were defined by gender.

Between male and female dolphins--Dominance relationships between male and female dolphins appeared to be determined by gender. Each male was consistently dominant to each female in all social groups. Overall, among adult and maturing dolphins, males won 95.9% of decided agonistic interactions with females (n = 2 males, 4 females, 831 decided interactions, Table 6*a-c*). Each male was also dominant to the juvenile female, Allie (n = 125 decided interactions, 0% reversals, Table 6*c*). The highest percentage of reversals was observed between the maturing female, Windy, and same-aged male, Stormy, during the first two years of the study (n = 260 decided interactions, 7.3% reversals, Table 6*a*).

Dominance of males over females was not strictly related to age or body size. Males dominated females who were both older and younger (Table 1). In addition, although the older male was consistently heavier and at least as long as females he dominated, the younger male, Stormy, was able to dominate females for several years prior to his 1991 attainment of greater body mass (than non-pregnant females) (Table 3). Prior to surpassing females in body mass, the younger male's involvement in agonism with females was disproportionately high. He was the male partner in 77% of all decided agonism with females during the first two years of the study (Table 6*a*). Moreover, during the first year of the study, Stormy's involvement in agonism with females was significantly higher (median rate = 0.036 per min) than Nemo's (median rate = 0.001)

(Mann-Whitney U = 11.5, P < 0.002, $n_1 = n_2 = 12$ mo). Rates at which males engaged in agonism with females did not differ during subsequent years.

Between male dolphins--The pair of males had an inconsistent dominance relationship during the 53-month study. Their relations may be interpreted as alternating back and forth (Table 7) or as transitional from subordinance to dominance by the younger male (Fig. 2). Changes in the males' relationship were detailed in Table 7. At the onset of the study, the older male, Nemo, was considered dominant member of the pair based on qualitative observations during the preceding two years (Samuels, unpublished data). During 1988, Nemo won a majority (67%) of decided agonistic interactions but was routinely challenged by the younger male. The males rarely engaged in agonism until the fall of 1988 when several outbreaks of aggression between the males occurred at the same time that Nemo's health declined, resulting in his separation from the group for nearly two months (Table 2). Following Nemo's reintroduction in February 1989, Stormy won a clear majority of decided agonistic interactions (79%) for the remainder of 1989.

By January-February 1990, however, neither male could be identified as dominant, *i.e.*, each won approximately 50% of decided interactions. For the duration of 1990, the males alternated which one was dominant every one to three months. During this changeable 12-month period, the rate of male *vs.* male agonism was higher (overall 1990 rate = 0.048 interactions per min) than during any other year of the study (overall rate for all other years = 0.0165) (Mann-Whitney U = 81, z = 3.45, P < 0.0003, $n_1 = 12$ mo in 1990, $n_2 = 40$ mo in all other years). Moreover, more than half of all decided agonistic interactions between males occurred during 1990 (Fig. 2).

By January 1991 until the end of the study in May 1992, the younger male, Stormy, again consistently dominated Nemo, winning 88% of dominance interactions.

Periods of instability between males (*i.e.*, periods in which neither won > 75% of decided interactions) corresponded to periods in which they engaged in high proportions of undecided interactions. Specifically, the proportion of male *vs.* male agonism that was undecided was significantly lower in stable periods (median = 0.36) than in unstable periods (median = 0.615) (Mann-Whitney U = 0, P = 0.028, $n_1 = 2$ unstable periods (January-December 1988, January-February 1990), $n_2 = 7$ stable periods (Table 7)).

Stormy's ultimate attainment of dominance by 1991-1992 coincided with his attainment of comparable body mass to that of the older male. Neither male showed appreciable change in body length during 1986-1992; however, whereas Nemo's body mass did not change substantially during 1988-1992, Stormy exhibited a 20-kg increase in body mass during the same period (Table 3).

Between female dolphins--Females had stable dominance relationships that appeared to be related to age. Although mature females rarely engaged in agonism with each other, outcomes of decided interactions were consistent over periods of > 1 yr. Dominance relations of two Group 1 females corresponded to their age order: adult Angie was dominant to maturing Windy, winning 88% of dominance interactions (Table 8*a*). Dominance relations of four Group 3-4 females also corresponded to age order: > 20-yr-old Connie was dominant to teen-aged Windy, who dominated 10-yr-old Tapeko, who dominated juvenile Allie (Table 8*b*). Low-ranking juvenile, Allie, was the most common partner in agonistic interactions, being involved in 82% of decided and 90% of undecided agonism among Group 3-4 females.

Age, but not body size, appeared to influence dominance relations among females. In Group 1 dominant Angie was longer but had similar body mass to younger, subordinate Windy (Table 3). In Group 3-4, dominant Connie was shorter and had substantially less body mass than second- and third-ranked younger adults, Windy and

Tapeko, whose body dimensions were comparable to each other; low-ranking juvenile, Allie, was shorter and had smaller body mass than adults who dominated her (Table 3).

Between female dolphins during a brief introduction--Although agonism among familiar females was typically low level, a high rate of agonism occurred during a 16-day introduction of two pairs of females. During the introduction, females engaged in agonistic interactions approximately once every 24 min (0.042 interactions per min). Residents, Angie and Windy, were dominant to newcomers, Rio and Mindy (Table 8*c*), although the relative status of Windy and older Rio may have been in transition by the end of the introduction. All decided interactions were directed towards a member of the opposing pair and none occurred within pairs of long-term associates (Table 8*c*).

Seasonal Patterns of Agonism

Seasonal patterns were detected in rates of agonism among adult and maturing dolphins. For agonism between males and females, there was a clear seasonal pattern during 1988 and 1990, with a summer period (June-August) of negligible agonism bounded by elevated agonism both in spring (April-May) and fall (September-October) (Fig. 3). Median monthly rates of male *vs.* female agonism were significantly correlated in these two years (Spearman Rank Correlation Coefficient $r_s = 0.82$, $P < 0.01$). The pattern was similar in 1989, despite heightened agonism throughout the year, with relatively lower rates in summer (June-July) and relatively higher rates in spring (April-May) and fall (September-October) (Fig. 3). Overall elevation of agonism in 1989 co-occurred with first-time conceptions of Angie and Windy. Some agonism peaks coincided with conceptions that occurred in the fall: August-September 1989 and September-October 1990 (Windy); month unknown 1989 (Angie).

A seasonal pattern was also evident for male *vs.* male agonism during 1988 and 1989, with a peak in agonism during October-December after negligible agonism during preceding months (Fig. 4). However, this pattern was absent in 1990 (compared with

1988: Spearman $r_s = 0.15$, ns), a year when agonism between males was consistently elevated (Fig. 4). Overall elevation of agonism in 1990 co-occurred with the males' intense competition with each other for dominance status (Fig. 2).

DISCUSSION

Dominance relationships among bottlenose dolphins at Brookfield Zoo were influenced by the gender of participants. Male dolphins were clearly and consistently dominant to females, and intersexual agonism occurred at moderate rates with seasonal peaks in spring and fall. Female dolphins had stable dominance relations that were ordered by age, even though agonism among females occurred at uniformly low rates. In contrast, the two males had a changeable dominance relationship in which periods of stability and low-level agonism were interspersed with episodes of intense competition. Undecided agonism occurred predominantly in dominance relationships that were in flux.

Patterns of dominance relations among BZ dolphins were consistent with observations at some other dolphin colonies, and with sex differences in competitive behavior of other mammalian species that share with dolphins certain aspects of social structure or life history. We discuss these comparisons in more detail and suggest that patterns of behavior detected in this zoo-based study may serve as models for better understanding social relations of wild bottlenose dolphins.

Dominance Relations among Captive Bottlenose Dolphins

Dominance relations among BZ bottlenose dolphins resembled some but not all reports from other dolphin colonies. We were able to resolve some discrepancies by reexamining conclusions derived from some earlier, non-quantitative studies.

Our finding that mature males were dominant to mature females was compatible with most other reports (*e.g.*, Essapian 1953; Tavolga 1966; Tayler and Saayman 1972). We found that suggestions to the contrary, *i.e.*, that females dominated males (*e.g.*,

Norris 1967), were not based on long-term relationships between adults. For example, adult females may dominate immature males (Tavolga 1966), adult females may aggressively prevent entry of new males into captive groups (Wood 1977), and adult females may win occasional agonistic encounters with adult males (Tayler and Saayman 1972; this study). In addition, it is often a high-ranking female, not the dominant male, who is perceived to be the center of social activity (*e.g.*, Tavolga 1966; Angie, this study), a social role that may be misconstrued as agonistic dominance.

Longitudinal monitoring of male *vs.* male dominance relationships, carried out at one other colony, revealed a pattern resembling the changeable dominance relations of BZ males. Specifically, initially-stable relations among three males at Marine Studios (McBride 1940; McBride and Hebb 1948) broke down within a year and two males were removed to reduce aggression (McBride and Kritzler 1951). Findings of shorter-term studies were mixed. Some male dominance relationships were changeable (Prescott 1977; Östman 1991), but stable relations were also reported in circumscribed relationships, *e.g.*, between adult and immature males (McBride and Hebb 1948), or between adult males captured together from the wild (McBride 1940; Tayler and Saayman 1972) who may have had previously-established dominance relations. In general, however, there were few descriptions with which to compare to the BZ males' relationship because colony managers typically try to prevent excessive aggression by including only a single adult male in breeding groups (Caldwell *et al.* 1968; Caldwell and Caldwell 1977; Wood 1977; Amundin 1986). For this reason, the younger male in this study was later removed from the BZ group.

Dominance relations among adult and maturing females at Brookfield Zoo were clear-cut and stable. The rare expression of agonistic dominance among familiar females contrasted strongly with a high rate of agonism among newly-introduced females who were establishing dominance relations. Dominance relationships among BZ females appeared to be related to age but were not strictly related to body size. Tayler and

Saayman (1972) also reported for a pair of adult females age-ordered dominance relations that persisted for several years.

Our finding that mature females had stable dominance relations diverged from prevalent views that female dominance relations were indistinct (Tavolga 1966; reviewed in Shane *et al.* 1986), that females did not aggressively compete with each other or form part of the hierarchy (McBride and Hebb 1948), or that a female's dominance status varied according to her mating partner (Tayler and Saayman 1972). Female dolphins, however, do behave aggressively (Saayman and Tayler 1977), particularly during introductions of strangers (McBride and Hebb 1948; Caldwell *et al.* 1968; this study). The perception that female dominance relations were indistinct (Tavolga 1966) likely ensued from the low rates of agonism among females when compared with those involving males (see below). Finally, the conclusion that normally stable, age-ordered dominance relations of two females varied in the context of sexual consortships (Tayler and Saayman 1972) was based on interactions that involved males rather than interactions solely among females.

Female agonism involving a juvenile was more commonplace than that among mature females. However, with only a single immature in the colony, we could not distinguish whether such elevated rates of agonism were due to juvenility or individual variation. Nonetheless, the result suggests caution in pooling observations of different age classes.

A seasonal component to agonistic behavior may correspond to the high degree of reproductive seasonality retained by female bottlenose dolphins despite long periods in captivity (Urian *et al.* 1996). Increased aggression in association with seasonal peaks in mating activity was reported at several colonies (*e.g.*, McBride and Kritzler 1951; Essapian 1963; Caldwell *et al.* 1968; Caldwell and Caldwell 1977). Among BZ dolphins, heightened male *vs.* female agonism in the fall co-occurred with fall

conceptions. However, there were no conceptions corresponding to elevated agonism in the spring, and without hormonal information, we could not conclusively link patterns of agonism with reproductive events.

Is Dominance an Artifact of Captivity?

Present knowledge about dolphin dominance relationships was derived entirely from zoo and aquarium studies. Lack of confirmation from wild populations has led to speculation that dominance relationships in dolphin colonies may be an artifact of captivity or expressed in the wild by spatial separation (*e.g.*, Norris 1967; Johnson and Norris 1986; Shane *et al.* 1986). Lack of verification from wild populations is not surprising, however, given the scarcity of cetacean field studies that focus on any aspect of social behavior. Moreover, spatial segregation of some age/sex classes within wild dolphin communities (Wells *et al.* 1987) does not preclude dominance relationships between individuals who interact on a regular basis.

Animals in naturalistic captive settings often exhibit behavior that approximates the patterns and contexts of social exchange in the wild. Thus, although rates of socializing may be higher in captive or food-provisioned groups (*e.g.*, primates: Nieuwenhuijsen and de Waal 1982; Altmann and Muruthi 1988; but see de Waal 1989), comparative captive and field studies have demonstrated that fundamental social patterns are often conserved in naturalistic captive environments. For example, kin-based relationships are prevalent in both captive and wild populations of many primate species (Gouzoules and Gouzoules 1987). As a specific example, matrilineal dominance relations are a pervasive feature of long-term groups whether they be captive, provisioned, or free-ranging (*e.g.*, cercopithecine primates: Sade 1967; Silk *et al.* 1981; Hausfater *et al.* 1982; Silk 1987; spotted hyaenas: Frank 1986; Jenks *et al.* 1995).

Retention of basic behavioral patterns has also been reported for captive delphinids (*e.g.*, *Stenella* spp.: Wells 1984; Pryor and Kang Shallenberger 1991; Johnson

and Norris 1994; *Tursiops* spp.: Saayman and Tayler 1977). Similarly, we noted many parallels in the behavior of BZ dolphins and their wild conspecifics. For example, the BZ dolphins' social behavioral repertoire (including agonism) resembled, nearly behavior for behavior, that of wild *Tursiops* in Western Australia (Samuels, personal observation). Moreover, sex differences in ranging and association patterns of BZ dolphins mimicked on a small scale those described for wild dolphins (Wells *et al.* 1987, Scott *et al.* 1990, Wells 1991, Connor *et al.* 1992, Smolker *et al.* 1992). For instance, in the early morning prior to human-focused activity, the two BZ males typically swam together as a unit and ranged throughout the entire pool complex, whereas BZ females exhibited more restricted ranging patterns and had preferential but less consistent associations with other females (Samuels, unpublished data). In addition, the bimodal pattern of male *vs.* female agonism among BZ dolphins corresponded to the late spring and early fall breeding peaks of wild Florida *Tursiops* (Wells *et al.* 1987). These similarities suggested that patterns of dominance relations among captive dolphins are likely to resemble in fundamental ways those of their wild counterparts. Because captive environments can take a variety of forms, some more naturalistic than others, the extent to which this is true will be determined by the specifics of each captive setting (Wood 1986).

Research in captive settings has significantly contributed to understanding the behavior of many animals (*e.g.*, Kleiman 1992). For marine animals whose behavior is particularly difficult to observe in the wild, captive settings offer unique opportunities for behavioral research (Tavolga 1966; Defran and Pryor 1980; Pryor and Norris 1991; Samuels in press) and facilitate development of field behavioral research techniques (*e.g.*, Pryor and Kang Shallenberger 1991; Janson 1994). In the present study, the excellent visibility and close, consistent observation conditions enabled us to detect and determine the context of "flinch," a previously-undescribed submissive behavior that was integral to assessment of dominance relations. In addition, the ability to observe entire sequences of behavior, and to monitor long-term social relations of the same individuals, enabled us to develop and validate a quantitative technique for assessing dominance relations that

can be used in field research. Integration of captive and field studies in this way can provide a powerful tool for interpreting the behavior and social dynamics of a difficult-to-study animal like the bottlenose dolphin.

Sex Differences in Competitive Behavior

Behavioral parallels in captivity and the wild led us to suggest that patterns detected in this zoo-based study may serve as models for better understanding social relations of wild dolphins. This supposition was further supported by the concordance of observed patterns in dominance relations among BZ dolphins with sex differences in the behavior of wild bottlenose dolphins and other mammals that are similar in aspects of their social structure or life history.

The composite picture of dominance relations among captive male dolphins -- *i.e.*, that males had dominance relationships that were stable on a short-term basis but changeable over longer periods of time -- reflected a common pattern of agonistic relations among mammalian males. Even for species in which males form long-term coalitions with other males, allies can also be competitors who alternate which partner has priority of access to receptive females (bottlenose dolphins: Connor *et al.* 1992; chimpanzees: Nishida 1983).

Relevance of the BZ males' relationship as a model for relations among free-ranging male dolphins was suggested by other ways in which their relationship resembled that of male alliance partners in the wild. Typically, the BZ males were each other's preferred associate, they swam together as a unit, and they performed the elaborate "synchronous displays" described by Connor *et al.* (1992) (Samuels, unpublished data). Like their male counterparts in the wild, BZ males behaved as a coordinated unit at the same time that they were engaged in competitive encounters with each other. In the case of a single pair of males, however, we were unable to distinguish whether their changeable relationship represented a one-time maturational change -- as the younger

male's size, health status, and/or fighting ability surpassed that of the older male -- or exemplified changeable relations that might be typical among wild male dolphins.

Dominance of males over females is commonly reported among sexually-dimorphic species in which males are the larger sex (*e.g.*, baboons: Hausfater 1975; chimpanzees: Bygott 1979). Thus, male dominance in dolphins may be related to larger body-size dimensions and greater body mass of mature males over mature females, documented for wild *Tursiops* in Sarasota FL (Read *et al.* 1993; Tolley *et al.* 1995). In dolphin colonies, dominant males were typically the largest individuals (Essapian 1953; Tavolga 1966; Tayler and Saayman 1972); similarly, the older BZ male was heavier and as long or longer than the females he dominated.

The younger BZ male, however, was also able to dominate females prior to attaining greater body size, a pattern described for other male-dominant, sexually-dimorphic species (*e.g.*, baboons: Johnson 1987). Like maturing male baboons that typically dominate adult females before successfully competing with larger adult males (Pereira 1988), the younger male dolphin was dominant to all females in the group before he consistently dominated the older male. His high level of involvement in agonism with larger females resembled elevated rates of aggression exhibited by immatures of some primate species when competing for adult dominance status (Walters and Seyfarth 1987): *e.g.*, as adolescents, chimpanzee males display heightened aggression towards adult females (Pusey 1990). In addition, the younger male dolphin's ability to defeat larger females in one-on-one agonistic interactions may have been linked to his close relationship with the older male and the males' tendency to sometimes act as a unit in polyadic, two-on-one agonistic encounters with females (Samuels, unpublished data). Their coordinated agonistic efforts resembled the behavior of allied male dolphins in the wild who cooperate to aggressively sequester females (Connor *et al.* 1992).

Heightened agonism among females during an introduction contradicted an older

notion that female dolphins do not compete aggressively (*e.g.*, McBride and Hebb 1948). Female chimpanzees, who have similarly stable and infrequently-expressed dominance relations in captivity, also engage in intense competition when developing relationships with unfamiliar females (Baker and Smuts 1994). Female chimpanzees apparently do not often try to change their status once dominance relations are established (Baker and Smuts 1994), and this appeared to be the case for BZ female dolphins.

The stability of dominance relationships among BZ female dolphins conformed to a widespread pattern among female-philopatric mammalian species, in which residence of females within their natal group typically results in long-term, stable social relationships among females (*e.g.*, Wrangham 1980; Harcourt and Stewart 1983). Since long-term associations between individual females are characteristic of wild bottlenose dolphins (Wells *et al.* 1987; Scott *et al.* 1990; Smolker *et al.* 1992), dominance relations of female dolphins might be expected to reflect this stability.

Kinship is also a determinant of dominance relations among species in which female kin form long-term, close associations (*e.g.*, spotted hyaenas: Frank 1986; baboons: Hausfater *et al.* 1982; bonnet macaques: Silk *et al.* 1981). Although kinship has been identified as a significant factor in determining long-term associations among female bottlenose dolphins (Wells *et al.* 1987; Duffield and Wells 1991; Smolker *et al.* 1992), we were unable to evaluate the relative influence on female dominance relations of kinship *vs.* age because BZ females were unrelated. However, the introduction of two pairs of females highlighted the tendency of female dolphins to ally themselves with familiar females in confrontations with strange females. Introduced pairs, each of which was composed of long-term associates, sometimes behaved as units such that familiar females supported each other in agonistic encounters with strangers (Samuels, unpublished data).

Contributions of Quantitative Behavioral Sampling Techniques

We consider the demonstration of effective use of quantitative sampling techniques in cetacean behavioral research to be an important result of this study. A historical example illustrates how such techniques may advance understanding of cetacean societies. Until the 1980s, it was commonly held in the field of animal behavior that males were responsible for determining the structure of many animal societies, and there was correspondingly little interest in the behavior of females (Fedigan 1982; Hrdy and Williams 1983). Male-focused views were initially due to theoretical biases and further promoted by descriptive behavioral research methods that tended to amplify the significance of eye-catching, aggressive patterns of male behavior and to diminish the importance of less conspicuous patterns of female behavior.

With shifts in theoretical emphases and with development of methodologies to minimize biases due to conspicuousness of behaviors or age/sex classes (Altmann 1974), many male-focused views were rejected. For example, following the transition from descriptive, natural history (*e.g.*, DeVore 1965) to long-term, quantitative behavioral studies of known individuals (*e.g.*, Smuts *et al.* 1987), primatologists revised their perception of baboon society from one "organized around the dominance hierarchy of adult males" (Hall and DeVore 1965:54) to one in which kin-based groups of females formed the stable core (*e.g.*, Hausfater *et al.* 1982). Female baboons, previously thought to have nonexistent or inconsistent dominance relationships that varied with reproductive status (Hall and DeVore 1965), were subsequently found to have dominance relations that were stable, long-term, and based on kinship (Hausfater *et al.* 1982).

Descriptive research methods, and resultant anecdotal accounts of social relations, were also commonplace in early studies of dolphin behavior. Unfortunately, despite an up-dated theoretical framework in cetacean biology (*e.g.*, Le Boeuf and Würsig 1985) and better knowledge about *Tursiops* social structure (*e.g.*, Wells *et al.* 1987, Smolker *et al.* 1992), use of contemporary behavioral research methods has not been widespread.

Because only a single quantitative study of dolphin dominance relations has been conducted in recent years (Östman 1991), perceptions of dolphin agonistic relations (*e.g.*, Shane *et al.* 1986) have necessarily been derived from older, qualitative studies that emphasized a male-dominated social structure, and correspondingly, dismissed female agonistic relationships as unimportant or inconsistent. Use of *ad libitum*, descriptive methods in the early studies likely emphasized the conspicuous aggression of males over low-level agonism of females; thus, conclusions of those studies were likely to have been more comprehensive with respect to agonism involving males and more subjective regarding dominance relations among females. Our suggestion that *ad lib.* methods contributed to a mistaken impression of female agonistic relations is supported by our observation that the sole early report of stable dominance relations between females (Tayler and Saayman 1972) was based on a group in which males (and their distracting behavior) were absent for several years.

In contrast, use of quantitative behavioral sampling techniques in this study revealed dominance relationships that better conformed to current knowledge about the social structure of bottlenose dolphins and broader mammalian patterns. In the spirit of promoting greater dialogue between field and captive research, we propose several predictions about the behavior of wild bottlenose dolphins based on results of our zoo-based study. (1) Although adult male and female dolphins typically are spatially segregated, we predict that when they do associate, individual males are dominant to individual females. (2) In addition to interalliance competition, we predict that male dolphins within alliances also engage in competitive interactions that result in changeable dominance relationships. (3) Finally, we predict that female dolphins who interact on a regular basis have long-term, stable dominance relationships.

Using these quantitative techniques, our predictions about dolphin dominance relations can be systematically evaluated in both captive and field research. Future studies may clarify, for example, the role of kinship or polyadic interactions in

determining dolphin dominance relations, and the relationship between dominance and reproductive success or access to resources. As proved true in the field of primate behavior, we predict that widespread application of quantitative behavioral sampling techniques in long-term studies of known individuals will move us towards a better understanding of social behavior of cetaceans.

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Table 1: Brookfield Zoo bottlenose dolphin colony during January 1988-May 1992: dolphins are listed by sex, age, and order of joining the colony. All dolphins were wild-caught as immatures except captive-born Allie; all resident dolphins originated from Florida waters except Connie (Texas). Maturational classifications are explained in the text.

	Dolphin Name	Residence during study	Age[1] and Maturational Class		Demographic Events
	Long-term Residents				
♂	Nemo	January 1988-May 1992	15-19 yr	adult/ maturing	
	Stormy	January 1988-May 1992	11-15 yr	adult/ maturing	
♀	Angie	January 1988-January 1990	30+ yr	adult	First conception, fall 1989 Died, January 1990
	Windy	January 1988-May 1992	11-12 yr 13-15 yr	maturing adult	First conception, August-September 1989 Conception, September-October 1990
	Tapeko	March 1991-May 1992	9-10 yr	adult	Arrival, March 1991 First conception, April-May 1991
	Connie	July 1991-May 1992	20+ yr	adult	Arrival, July 1991 Conception, fall 1991[3]
	Allie	July 1991-May 1992	4-5 yr	juvenile	Arrival, July 1991
	Short-term Visitors				
♀	Rio	none[2]	15+ yr	adult	
	Mindy	none[2]	13+ yr	maturing	

[1] Ages of dolphins were based on known birthdate of the captive-born female (Allie) or estimates from body length at time of capture for wild-born dolphins (T. Hughes, E. Krajniak, K. Krieger, personal communications; NMFS 1995, unpublished data). Growth patterns of known-age wild bottlenose dolphins indicated that such age estimates based on immature body length were likely to be accurate to within $\pm$ 2 yr (Read *et al.* 1993).
[2] Minnesota Zoo females, Rio and Mindy, were temporarily housed at Brookfield Zoo during October 1989-April 1990. During January 1990, they were introduced to resident females, Angie and Windy (see text).
[3] Connie's first conception occurred at another facility prior to her arrival at Brookfield Zoo.

Table 2: Dolphin social groupings during the study. Each dolphin's name is annotated to indicate its maturational class at that time: [a] = adult, [m] = maturing, [j] = juvenile.

Group	Dates	Duration (months)	Group Composition ♂♂	♀♀
1	January 1988-January 1990	25[1]	Nemo[2 m/a], Stormy[m/a]	Windy[m/a], Angie[a]
2	February 1990-February 1991	13	Nemo[m/a], Stormy[m/a]	Windy[3 a]
3	March 1991-June 1991	4	Nemo[m/a], Stormy[m/a]	Windy[a], Tapeko[a]
4	July 1991-May 1992	11	Nemo[m/a], Stormy[m/a]	Windy[3 a], Tapeko[3 a], Connie[a], Allie[j]

[1] Group 1 dolphins had been together since at least 1979.

[2] Nemo was temporarily separated from the main group during December 1988-February 1989 due to illness and aggression between the males. Females (who knew how to jump over the net barrier) freely visited each male.

[3] Expectant mothers, Windy and Tapeko, were each separated temporarily from the main group for calving, sometimes with another female. Although infants born during the study did not survive to join the main group, both females have subsequently produced surviving offspring.

Table 3: Body size measurements of dolphins[1].

Sex	Dolphin	Body Length (cm)		Body Mass (kg)		
		1986[2]	1991-1992[3]	1988-1989[5]	1991[6]	1992[8]
♂	Nemo	259	259	204.1	200.5	201.8
	Stormy	249	249	173.7	192.8	195.5
♀	Angie	259[4]	--	187.8	--	--
	Windy	244	249	187.3	192.8[7]	180.1
	Tapeko	--	246	--	195.9[7]	184.2
	Connie	--	234[4]	--	--	149.2
	Allie	--	229	--	--	145.6

[1] Body size measurements were taken opportunistically during medical examinations or transports until July 1992 when dolphins were trained to position for voluntary weighing.
[2] Median of two measurements per dolphin taken in March and October 1986.
[3] Single measurement per dolphin taken in March 1991 (Nemo, Stormy, Windy, Tapeko) or in October 1992 (Allie).
[4] Lengths of two > 20-yr-old females were approximated by measurements taken outside of the study period (*i.e.*, Angie in 1986; Connie in November 1993). These were likely to be reliable estimates of each female's length during the study because females in Sarasota FL typically achieved asymptotic body length at an earlier age (Read *et al.* 1993).
[5] Median of two measurements per dolphin taken in October 1988 and May 1989.
[6] Median of two measurements per dolphin taken in March and June 1991 (Windy: March only).
[7] Body mass measurements were taken during early and middle pregnancy for Tapeko and Windy, respectively.
[8] Median of 3-17 measurements per dolphin taken during August-September 1992.

Table 4: Agonistic behaviors used to identify and evaluate dominance interactions (defined in text). Behaviors are listed within categories in approximate order of increasing severity. References indicate reports of delphinids (especially *Tursiops* spp.) exhibiting similar behaviors.

Category	Behavior	Definition	References
Aggression	Threat	Opened mouth directed at another; often with abrupt, vertical head movement; sometimes with abrupt closure of jaw accompanied by loud sound (jawclap)	1,3,4,5,6,7,8,9,10,11,12,13,14, 15,16,17,18,19,20,21,22,23,24
	Chase	Rapid and persistent pursuit of another, usually accompanied by threats	1,3,4,6,7,8,11,15,16,18,19,20, 22
	Pin	Hold another on bottom, usually by lying over the other's body	2,3,15,21
	Ram	Abrupt and forceful contact with another using rostrum or melon	1,2,3,7,9,11,12,13,15,17,18
	Hit	Abrupt and forceful contact with another using tail or peduncle	1,4,7,8,9,10,12,13,14,15,17,18, 19,20,21,22
	Body Slam	Abrupt and forceful contact with another using torso, side of body, or dorsal fin	4,16,17,18
	Bite	Abrupt and forceful contact with another using teeth, sometimes resulting in rake marks	2,3,4,5,7,8,9,11,12,13,14,15, 18,19,20,21,22
Submission	Flinch	Immediate cringe, cower, or recoil in response to action of another; typically in the form of an abrupt movement of one or more body parts (*e.g.*, head, side) away from the other animal	8?,15?
	Flee	Abrupt, rapid, and immediate departure to $>$ 1 m in response to action of another; includes: leap above water, beach out of water, or flee to another pool	4,6,7,15,16,18,21

[1] Bateson 1974; [2,3] Caldwell and Caldwell 1967, Caldwell *et al.* 1968; [4] Connor *et al.* 1992; [5] Defran and Pryor 1980; [6,7,8] Essapian 1953, 1962, 1963; [9] Johnson and Norris 1986; [10] Lawrence and Schevill 1954; [11,12] McBride 1940, McBride and Hebb 1948; [13] Norris 1967; [14,15] Östman 1991, Östman, unpublished ethogram; [16] Overstrom 1983; [17,18] Pryor 1973, Pryor and Kang 1980; [19] Saayman *et al.* 1973; [20,21] Tavolga 1966, Tavolga and Essapian 1957; [22] Tayler and Saayman 1972; [23] Wood 1953; [24] Würsig *et al.* 1990.

Table 5: Rules for evaluating the outcome of agonistic interactions [adapted from Hausfater (1975)]. See text for further explanation.

Agonism Type	% All Agonism	Action by:		Identity of Winner	% per Agonism Type
		Dolphin A	Dolphin B		
Decided	59%	Aggression	Submission	Dolphin A	69%
		Neutral	Submission	Dolphin A	31%
Undecided	41%	Aggression	Neutral	Neither	66%
		Aggression	Aggression	Neither	18%
		Aggression	Aggression+ Submission	Neither	13%

Table 6: Dominance matrices of male *vs.* female dolphins, based on 956 decided agonistic interactions (3.6% reversals). Dolphins are listed by age within sex classes. The value of a cell is the number of times the dolphin in that row (winner) won a decided interaction with the dolphin of that column (loser). Interactions between same-sex partners are shown elsewhere.

(a) Group 1 (January 1988-January 1990): n = 485 interactions, 5.4% reversals.

		Loser			
		♂ Nemo	♂ Stormy	♀ Angie	♀ Windy
Winner	♂ Nemo	--	--	39	69
	♂ Stormy	--	--	110	241
	♀ Angie	1	2	--	--
	♀ Windy	4	19	--	--

(b) Group 2 (February 1990-February 1991): n = 135 interactions, 1.5% reversals.

		Loser		
		♂ Nemo	♂ Stormy	♀ Windy
Winner	♂ Nemo	--	--	98
	♂ Stormy	--	--	35
	♀ Windy	0	2	--

(c) Group 3-4 (March 1991-May 1992): n = 336 interactions, 1.8% reversals.

		Loser					
		♂ Nemo	♂ Stormy	♀ Connie	♀ Windy	♀ Tapeko	♀ Allie
Winner	♂ Nemo	--	--	38	44	39	75
	♂ Stormy	--	--	7	34	43	50
	♀ Connie	1	0	--	--	--	--
	♀ Windy	1	1	--	--	--	--
	♀ Tapeko	0	3	--	--	--	--
	♀ Allie	0	0	--	--	--	--

Table 7: Changes in the dominance relationship of two male dolphins from January 1988 through May 1992, based on 219 decided agonistic interactions.

	Dates	# Months	# Decided Interactions	Percentage Won	Dominant Male
1988	January-December	12	12	67%	Nemo?
1989	February-December	11	53	79%	Stormy
1990	January-February	2	19	53%	None
	March-April	2	11	100%	Nemo
	May- August	4	35	83%	Stormy
	September	1	12	92%	Nemo
	October-November	2	21	76%	Stormy
	December	1	16	88%	Nemo
1991-1992	January-May	17	40	88%	Stormy

Table 8: Dominance matrices of female dolphins in two stable social groupings (*a* and *b*) and during a brief introduction of two pairs of strangers (*c*). Row and column conventions as in Table 6. See text for further explanation.

(a) Group 1 (January 1989-January 1990): n = 43 interactions, 11.6 % reversals.

		Loser	
		♀ Angie	♀ Windy
Winner	♀ Angie	--	38
	♀ Windy	5	--

(b) Group 3-4 (April 1991-May 1992): n = 80 interactions, 6.2 % reversals.

		Loser			
		♀ Connie	♀ Windy	♀ Tapeko	♀ Allie
Winner	♀ Connie	--	2[1]	8	10
	♀ Windy	0	--	3	17
	♀ Tapeko	1	0	--	35
	♀ Allie	2	1	1	--

(c) Brief introduction of residents, Angie and Windy, to unfamiliar females, Rio and Mindy (12-26 January 1990): n = 40 interactions, 12.5% reversals.

		Loser			
		♀ Angie	♀ Windy	♀ Rio	♀ Mindy
Winner	♀ Angie	--	0	16	5
	♀ Windy	0	--	11	3
	♀ Rio	0	5	--	0
	♀ Mindy	0	0	0	--

[1] The only decided agonistic interactions observed between Connie and Windy occurred during the first week of their introduction.

Figure 1. Mean rate (per min) of agonism involving adult and maturing dolphins, partitioned by partner type: male *vs.* male, male *vs.* female, and female *vs.* female. Brackets denote standard error.

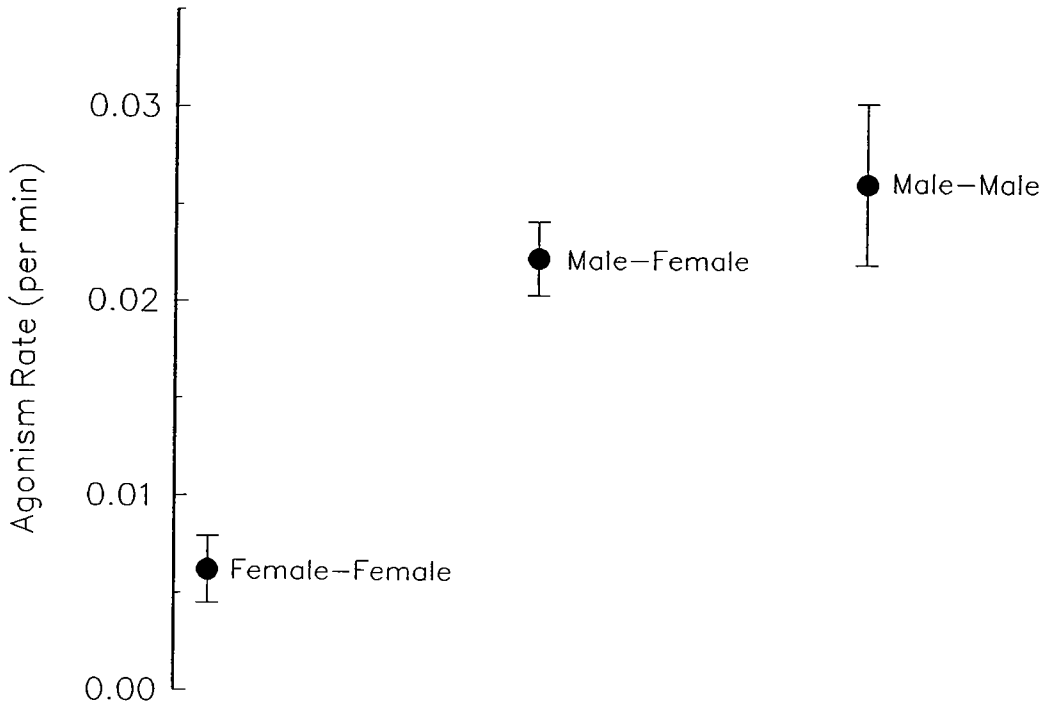

Agonism Rate (per min)
0.03
0.02
0.01
0.00
Female–Female
Male–Female
Male–Male

Figure 2. Number of decided agonistic interactions won by each male during each year of the study.

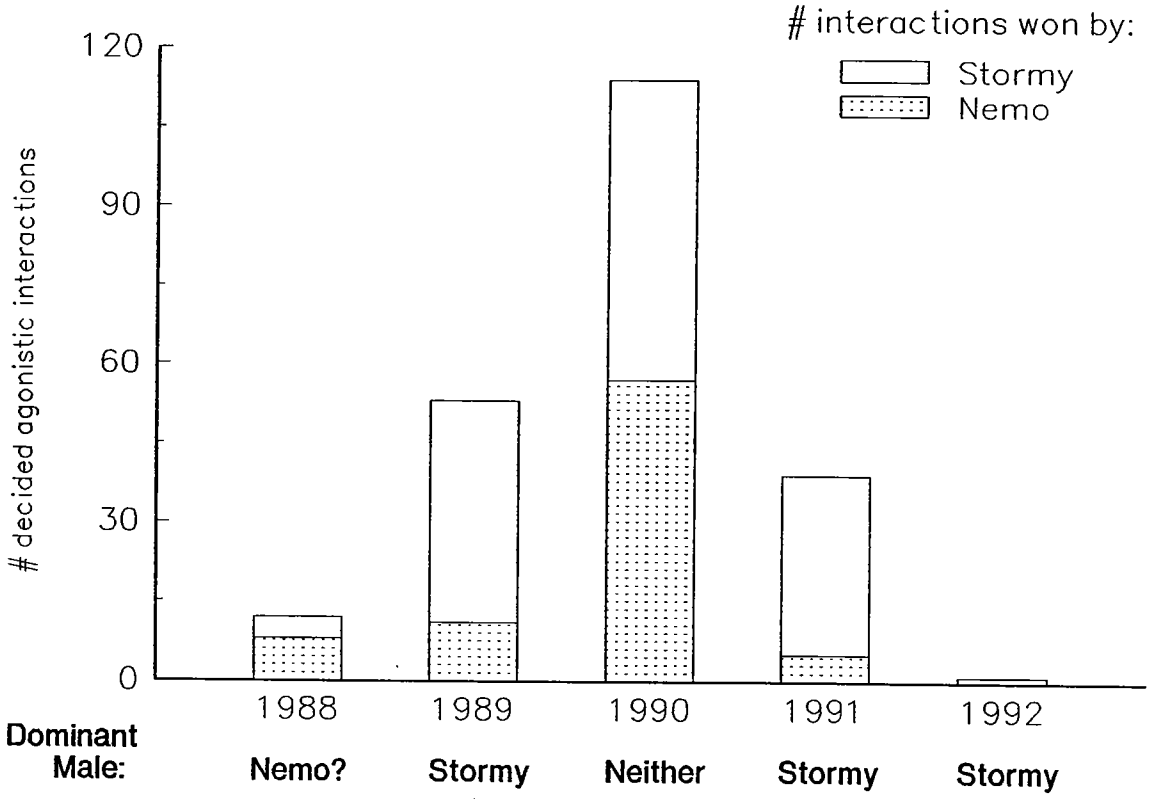
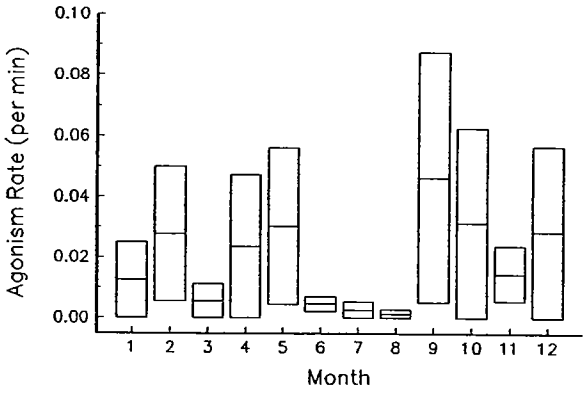
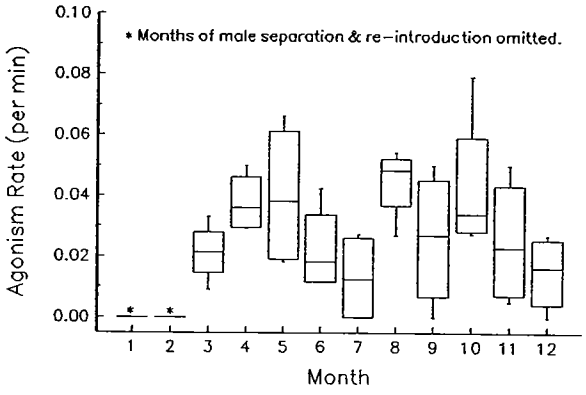

interactions won by:
Stormy
Nemo
120
90
60
30
0
decided agonistic interactions
1988
1989
1990
1991
1992
Dominant Male:
Nemo?
Stormy
Neither
Stormy
Stormy

Figure 3. Box plots of monthly male *vs.* female agonism rates (per min) among adult and maturing dolphins per year (1988-1990). Plots indicate median monthly rates and 25% quartiles.

1988



1989



1990

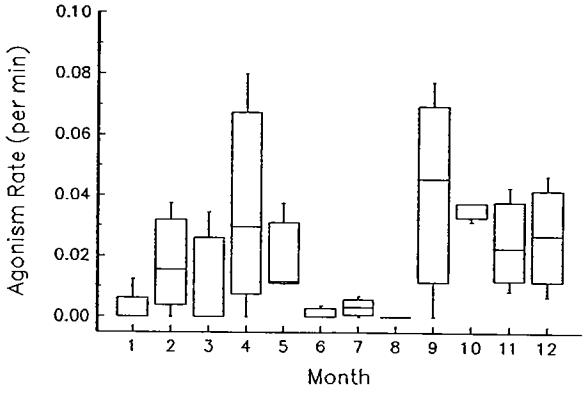
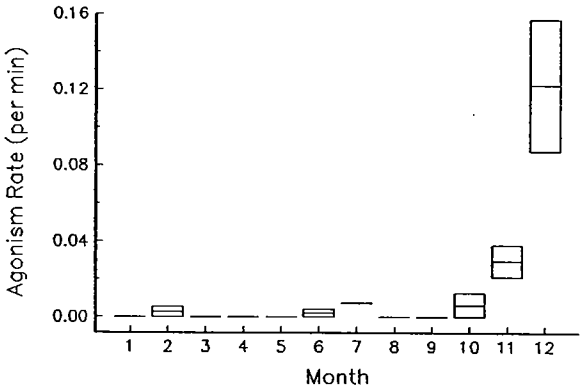
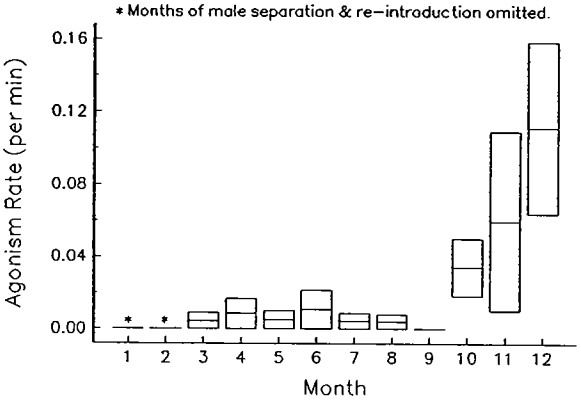


Figure 4. Box plots of monthly male *vs.* male agonism rates (per min) among adult and maturing dolphins per year (1988-1990). Conventions as in Fig. 3.

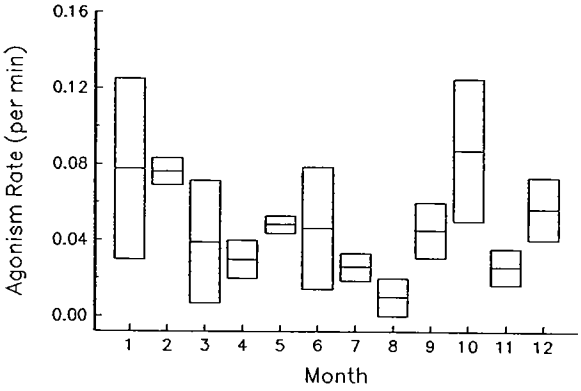
1988



1989



1990



CHAPTER 3. SEX DIFFERENCE IN THE ASSOCIATION OF WILD JUVENILE BOTTLENOSE DOLPHINS WITH THEIR MOTHERS

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ABSTRACT

Female juvenile bottlenose dolphins continued to associate with their mothers for several years following weaning. In contrast, juvenile sons rarely spent time with their mothers after independence even though they apparently remained in the same general area. Preliminary results suggested that the broader social network of juvenile males may be quite different from that of their female counterparts. One juvenile male had as his top-ranked associates several same-aged males, whereas the primary social associates of three juvenile females included their mothers as well as other same-aged and adult females. Sex differences in the social associates of juvenile dolphins appear to foreshadow their adult social networks.

INTRODUCTION

Juvenile animals are those capable of surviving without parental provisioning but who are not yet able to reproduce. For mammals, this life stage begins with weaning from mother's milk and ends with onset of sexual maturation (Pereira and Altmann 1985). This stage is considered one of "phenotypic limbo" (Pagel and Harvey 1993: 28) in which an individual's age, size, and experience are adequate to sustain independent life but not yet sufficient to enable reproduction.

The length of the juvenile period varies among mammals. Female Mongolian

gerbils can have fertile matings before they are weaned, thereby by-passing a juvenile phase altogether (Clark *et al.* 1986). In contrast, some other species have lengthy juvenile periods that are several years long (*e.g.*, African elephants: Laws and Parker 1968; chimpanzees: Goodall 1986). For some primates, the juvenile period can encompass up to 25% of the post-weaning life span (Pereira and Fairbanks 1993*b*).

Evolution of the juvenile period

Why do some organisms delay onset of their reproductive careers? Existence of a prereproductive period beyond parental care, and particularly one that is prolonged, requires explanation in the context of natural selection which favors earliest possible reproduction (Charlesworth 1980). Several schools of thought have attempted to explain the diversity of life-history tactics, including those traits that determine the length of the juvenile period: age at weaning and age at onset of sexual maturation. One school regards developmental schedules as adaptive consequences of an organism's allocation of finite resources among maintenance, growth, and reproduction in ways that maximize lifetime reproductive success (*e.g.*, Gadgil and Bossert 1970; Stearns 1976; Charlesworth 1980). Sexual maturation, the endpoint of the juvenile period, is pivotal in this disbursement of resources: at puberty, reproduction becomes a competitor for energy previously devoted to growth and maintenance (*e.g.*, Stearns 1992).

Under this interpretation, age at sexual maturation is viewed as a trade-off between age-specific rates of fecundity and mortality (*e.g.*, Gadgil and Bossert 1970; Stearns and Crandall 1981; Harvey *et al.* 1989). Early maturation may provide a head start to a reproductive career, but if young breeders are too small or inexperienced, their survival or reproductive success will be jeopardized. Delayed maturity is favored when deferred reproduction results in improved fecundity and/or survivorship rates (*e.g.*, Stearns and Crandall 1981; Stearns 1992; Rubenstein 1993) or when reproductive success is influenced by age, size, or social status (Stearns 1976).

An alternative interpretation is derived from cross-species correlations between life-history tactics and body size (*e.g.*, Western 1979; Western and Ssemakula 1982). Mammals can be arranged on a "fast-slow continuum" (*e.g.*, Stearns 1983) with large, long-lived, slowly-reproducing animals at one end and small, short-lived, prolific breeders at the other. Such correlations suggest that life-history variables are imposed by the allometric consequences of body size.

Under this interpretation, delayed maturation and prolonged juvenile periods are not primary products of selection but merely by-products of the time it takes for large-bodied animals to attain sufficient size to reproduce (*e.g.*, Western 1979; Western and Ssemakula 1982; reviewed in Read and Harvey 1989). However, many important correlations among life-history traits persist even after effects of size are removed (*e.g.*, Gaillard *et al.* 1989; Read and Harvey 1989), and the variation in life-history tactics found within species is often unrelated to size (reviewed in Harvey *et al.* 1989). Strong correlations between mortality and body size led Harvey *et al.* (1989) to suggest that body size may have been a surrogate for mortality rates in earlier analyses.

Being a juvenile may entail more than simply waiting to develop the body size and physiological machinery for successful reproduction. For primates, the juvenile stage is a time of learning about complex physical or social environments (*e.g.*, Pereira and Altmann 1985), and Harvey *et al.* (1987) suggested that postnatal brain development, learning, and social maturation may be closely linked to physical maturation. Some have proposed that delayed maturation evolved to provide opportunities for learning (*e.g.*, Poirier and Smith 1974; Gavan 1982). However, even if learning is no more than an artifact of extended growth, lengthy juvenile periods may nevertheless enable acquisition of behavioral and social skills: individuals that make wise use of their time in phenotypic limbo are likely to be better equipped for adult life (Pereira and Altmann 1985; Pagel and Harvey 1993; Fairbanks 1993).

Behavior of juvenile mammals

How do juveniles go about accomplishing their primary tasks of survival and preparation for adulthood? Despite the interest of life-history theorists in this life stage, the behavior of juvenile mammals has received relatively little attention. The reasons for this omission are several. Juveniles typically lack distinctive markings, and in many species, they move in boisterous, seemingly amorphous groups; therefore, from a practical standpoint, juveniles are more difficult to study than other classes (Rowell 1993). In addition, due to the influences of sociobiology, behavioral research has focused on short-term measures of reproductive success; thus, studies of adult mating strategies or parent-infant relations have taken precedence over studies of juvenile development (Pereira and Fairbanks 1993*b*).

Over the past two decades, an emphasis on long-term study of individually-identified animals has resulted in advances in knowledge about adult behavior and social relations which, in turn, have provided a framework for research on juvenile behavior and developmental strategies (*e.g.*, bison: Green *et al.* 1989; Rothstein and Griswold 1991; feral horses: Rubenstein 1982). Among the best-studied juveniles are primates (*e.g.*, Pereira and Fairbanks 1993*a*), notable even among "slow-living" mammals for their unusually long prereproductive periods (*e.g.*, Harvey *et al.* 1987).

Primatologists debate about the extent to which juveniles invest in current survival *versus* future gains (*e.g.*, Pereira and Altmann 1985; Janson and van Schaik 1993). The complex social and demographic conditions that each immature encounters can have dramatic effects on its development and its behavior as an adult (*e.g.*, Harcourt and Stewart 1981; Rubenstein 1982). Relationships with the mother often persist beyond physical dependency, and continued maternal investment is likely to be important in many respects, including juvenile survival (*e.g.*, Pusey 1983; van Noordwijk *et al.* 1993) and acquisition of social status (*e.g.*, Cheney 1977; Pereira 1989). Sex differences in adult behavior are often presaged in the activities of juveniles, and frequently emerge

prior to expression of the physiological demands (*e.g.*, Fairbanks 1993; van Noordwijk *et al.* 1993; reviewed in Pereira and Altmann 1985). Juvenile primates not only practice behaviors that they will need later as adults (*e.g.*, play-fight: Fagen 1993; interactions with infants: Fairbanks 1993), but they also develop long-term social relationships that may be beneficial during their adult lives (*e.g.*, Cheney 1978; Fairbanks 1993).

Social development of juvenile bottlenose dolphins

Among cetaceans, odontocetes are also "slow-living" with protracted prereproductive periods (*e.g.*, killer whales: Olesiuk *et al.* 1990; short-finned pilot whales: Kasuya and Marsh 1984; sperm whales: Best *et al.* 1984; but see, harbor porpoises: Read and Hohn 1995). Brodie (1969) contrasted the typical odontocete lifestyle with that of the faster-paced mysticetes (*e.g.*, cetaceans (primarily mysticetes): Gaillard *et al.* 1989; humpback whales: Clapham 1994), and he proposed that the prolonged lactational periods of toothed whales may provide opportunities for calves to learn about complexities of odontocete navigational systems and social structures. The extended juvenile period of odontocetes may serve similar functions.

Among odontocetes, the bottlenose dolphin (*Tursiops* spp.) has a lengthy prereproductive phase including a juvenile period of several-years duration (Wells *et al.* 1987; see "Methods" below). Longitudinal research on coastal populations of bottlenose dolphins in Florida (*e.g.*, Wells *et al.* 1987; Scott *et al.* 1990; Wells 1991) and in Western Australia (*e.g.*, Connor *et al.* 1992; Smolker *et al.* 1992) presents an opportunity for investigation of the behavioral development of individually-identified, known-age, known-sex juveniles within known social and demographic contexts.

Preparation for adult social life may be important for juvenile bottlenose dolphins who grow up within a complex, fission-fusion society. Adult association patterns are variable on a day-to-day basis but feature close, same-sex, long-term relationships (*e.g.*, Wells *et al.* 1987; Smolker *et al.* 1992). Adult male dolphins form stable bonds with

one or two other males that persist for many years, and males within a unit tend to behave cooperatively with each other (Wells *et al.* 1987; Connor *et al.* 1992). Adult females associate over a broader network of individuals while having close, long-lasting relationships with specific other adult females, including matrilineal kin (Wells *et al.* 1987; Scott *et al.* 1990; Smolker *et al.* 1992).

Although no studies have focused on the lives of juvenile dolphins, preliminary observations suggest that, after separation from the mother and prior to developing the adult relationships described above, juveniles preferentially associate with independent immatures of both sexes (Wells *et al.* 1987; Wells 1991; Smolker *et al.* 1992). These "subadult groups" tend to be age-segregated, biased towards male membership, and highly sociable (Wells *et al.* 1987; Wells 1991). Young males may associate within subadult groups until age 10-15 yr, wherein the tight bonds with one or several other young males are presumed to be formed (Wells 1991). Young females are also found in subadult groups but interact with adults as well, and at primiparity, resume associations within adult female networks, often that of their mother (Wells 1991).

The present study focuses on the wild juvenile dolphins of Shark Bay, Western Australia. The intricate and long-term nature of the social relationships of adult dolphins suggests that, as with some primate species, behavioral development of juvenile dolphins is likely to involve a slow process of integration into adult social networks. Differences in the associations of adult male and female dolphins suggest that behavioral sex differences may also be a feature of the social maturation of juvenile dolphins. Because continuing relations with the mother are crucial to maturation in many primate species, we examine the association of juveniles with their mothers as a first step in understanding the social development of juvenile bottlenose dolphins.

METHODS

Study site

The study site is an approximately 130 km^2 area in Shark Bay (25°47'S, 113°43'E) near Monkey Mia, a small camp in Western Australia. Shark Bay is well-known for long-term behavioral research on free-ranging bottlenose dolphins (*e.g.*, Connor and Smolker 1985; Connor *et al.* 1992; Smolker *et al.* 1992, 1993; Connor and Smolker 1995; Richards 1996; Connor *et al.* 1996). In addition, a small number of Shark Bay dolphins are famous for their frequent visits to Monkey Mia where they accept fish handouts from tourists (Connor and Smolker 1985; Wilson 1994).

Shark Bay is an exceptional site for research on social relations of dolphins because (a) the dolphins' residence patterns permit frequent, repeated sightings of known individuals; (b) longitudinal records of individual dolphins since the mid-1980s permit interpretation of behavioral patterns within known demographic, social, and matrilineal contexts; (c) habituation of dolphins to the proximity of researchers' boats permits close-up viewing of relatively-undisturbed social activity; and (d) clear-water conditions facilitate underwater viewing and use of quantitative observational techniques.

Shark Bay dolphins

The longitudinal database for the Shark Bay dolphin community is described in detail elsewhere (*e.g.*, Connor *et al.* 1992; Smolker *et al.* 1992). Briefly, individual dolphins are recognized by distinctive features of their dorsal fins, including fin shape and presence of nicks, holes, and scars. A catalog of dorsal fin photographs of more than 400 individually-identified dolphins is maintained for confirmation of identification. For the approximately 100 dolphins that are encountered on a regular basis, demographic information is available including sex, approximate age, and matrilineal kin.

The sex of many dolphins has been determined by observation of genital and anal slits, penis, or mammary slits. The genital region is clearly visible when dolphins swim

upside-down at the bow of a boat, as immatures in particular will readily do. For some older individuals, whose genital region was not observed, sex was surmised based on long-term association patterns that resemble those of an adult female (*i.e.*, persistent association with a calf) or those of an adult male (*i.e.*, persistent association with one or more known adult males).

The age of some dolphins is known precisely because they have been monitored since they were neonates. For other individuals, age was estimated during infancy by visual assessment of body size, behavior, fetal stripes, and/or other physical characteristics. For older individuals whose age was not estimated as infants, broad age classes ("juvenile/subadult" and "adult") were defined by body size and/or the extent of ventral speckling (as in Smolker *et al.* 1992).

Juvenile subjects

The juvenile life stage of bottlenose dolphins spans a several-year period beginning with nutritional independence from the mother and ending with onset of puberty. Subjects of this study were those immature dolphins identified as members of the juvenile class as determined by behavioral and age criteria. The age criterion for juvenile females was based on reproductive parameters estimated for females of the Shark Bay population (Richards 1996). This was compared with observations from the Florida field site where known-age, individually-identified *Tursiops* have also been monitored long-term (*e.g.*, Wells *et al.* 1987; Wells 1991) and with carcass analyses of Indian Ocean *Tursiops* killed in anti-shark nets off Natal (Cockcroft and Ross 1990). The age criterion for males was based on information from all three sites. Where there were discrepancies in the reported ages at which given developmental markers were attained, it was assumed that Shark Bay dolphins were more likely to resemble the *Tursiops* of Natal than the larger Florida form.

For subjects of this study, independence from the mother could be behaviorally

determined to occur when the immature ceased nursing, ceased such infantile behavior as swimming in "infant position" (*e.g.*, Smolker *et al.* 1993; Richards 1996), and was no longer in association with the mother for $\geq$ 80% of the time (Richards 1996). In Shark Bay, weaning never occurred before age 3.5 yr; infants were often dependent for 5-6 yr, and in one case, for at least 7 yr (Richards 1996).

The upper boundary of the juvenile period was more difficult to estimate precisely for individuals in the absence of behavioral or hormonal indicators. In some *Tursiops* populations, appearance of ventral speckles has been proposed as an indicator of the onset of puberty (Ross and Cockcroft 1990; Smolker *et al.* 1992). For example, ventral speckling is typically absent in immatures and present in mature dolphins off Natal (Ross and Cockcroft 1990). A small sample of similar observations strongly suggests that ventral speckling is correlated with sexual maturity (Smolker *et al.* 1992), but until the precise timing is worked out, we were reluctant to rely on this criterion.

The upper bounds of the juvenile period for Shark Bay dolphins were therefore estimated using age criteria. For females, earliest known age at first conception (*i.e.*, age at first birth minus 12-mo gestation) was used to estimate the upper limit of the juvenile period. Thus, for Shark Bay females, the end of the juvenile period was estimated to be no earlier than 11 yr of age (based on estimated age at first birth of 12-15 yr: Richards 1996). There was, however, only a single known-age, immature female older than 9 yr in our sample because monitoring of Shark Bay dolphins began relatively recently relative to their life span. Since her age was imprecisely known (see Table 1), we used 9 yr as the upper age limit for juvenile females in this analysis.

This age criterion for the upper boundary of the juvenile period of Shark Bay females concurs with the estimated age range for first ovulation (9.5-11 yr, n=3) based on ovarian scarring of Indian Ocean *Tursiops* off Natal (Cockcroft and Ross 1990). Florida females appear to mature somewhat earlier as indicated by a lower range of ages

at first birth (8-12 yr: Wells 1991). Hormonal monitoring is needed to determine whether defining the upper boundary of the juvenile period on the basis of first conception (or first birth) may erroneously include a period of "adolescent sterility" or anovulatory cycling (Short 1984).

An arbitrary upper age limit of 9 yr was chosen for Shark Bay juvenile males. Physical evidence for puberty is circumstantial: appearance of ventral speckling was reported for two Shark Bay males at ages 10 yr and 7.5+ yr (Smolker *et al.* 1992). This age range corresponds to the age at testicular enlargement of Natal *Tursiops*, occurring typically around 10-12 yr and less frequently at 9 yr (Cockcroft and Ross 1990). Florida males appear to attain puberty at a slightly younger age: based on body length and hormonal profiles, males considered to be "maturing" were 8-9 yr old (Wells *et al.* 1987).

Selection of subjects for this study was restricted to those juveniles (a) whose mother was known to still be living; (b) whose independence from the mother was known through observation or birth of a younger sibling; (c) whose sex was known through direct observation of the genital region; (d) whose year of birth was known or could be estimated to within 1-2 yr; (e) who was encountered on a regular basis; and (f) who did not accept fish handouts from humans. There were nine juveniles in the Shark Bay dolphin community who met these criteria during the present study: six females and three males aged 4 yr to approximately 9 yr (Table 1).

Data Collection and Analyses

Systematic sighting records were collected opportunistically at each encounter with dolphins within the study area. Sighting data were typically collected while researchers were searching for specified focal individuals (*e.g.*, adult females: Smolker *et al.* 1993; Richards 1996), or less often, during broader survey efforts. Sighting records have been collected since the mid-1980s (Smolker *et al.* 1992), but analyses of juvenile association

patterns utilized data collected during 1990-93 when monitoring was conducted year-round. Data analyzed herein were collected by the authors, R. Smolker, and K. Waples during September 1990 through August 1993.

Each sighting record was typically based on a brief encounter with dolphins and was roughly equivalent to a scan sample (Altmann 1974) in that information about the "group" (defined below) was recorded during the first 5 min of the encounter. Each record included identities of group members, location (triangulated from compass bearings taken on shore landmarks), and predominant activity state (*e.g.*, feed, travel, rest, socialize). Individual identity was confirmed by photographic documentation for all but the most commonly-sighted dolphins. These data were used to estimate the proportion of time each juvenile was in association with the mother. For a subset of subjects, we also evaluated each juvenile's primary social associates and its ranging pattern relative to that of the mother.

Analyses of association patterns followed conventions described in Smolker *et al.* (1992). For example, social groups of dolphins were considered to include all individuals within proximity that was defined by a 10-m chain rule, *i.e.*, each dolphin that was within 10 m of another (Smolker *et al.* 1992). Because certain activities were regarded as more indicative of preferential association patterns, groups of interest for these analyses were those in which the predominant activity was rest, slow-to-moderate-speed travel, or socializing. Feeding or rapidly-traveling groups were not included in these analyses because such aggregations tended to be more ephemeral, and therefore, less indicative of preferred association patterns (Smolker *et al.* 1992).

Estimates of the proportion of time that two individuals spent together were based on the "half-weight" association coefficient (Cairns and Schwager 1987), which yielded values ranging from 0 (dyads never sighted together) to 100 (dyads always sighted together). Juvenile subjects of this study and their mothers were selected because they

were among the most commonly-sighted, and therefore, best-documented individuals in the Shark Bay community; however, associates of some juveniles were sighted less frequently. Analysis of associates other than the mother was, therefore, restricted to the few, regularly-sighted juveniles whose associates were well-known; because of the limited sample, these results are considered to be preliminary.

Using data from 1990-1992, we approximated the ranging patterns of four juveniles (two males, two females) and their mothers using the method of minimum convex polygon: each juvenile's range was considered to be the area encompassed by connecting the outermost locational points (Stickel 1954). This method is adequate to assess whether each juvenile still lived in roughly the same area occupied by its mother, but may be less suitable for detailed analyses of ranging behavior (see, *e.g.*, Smith and Dobson 1994).

Because births in Shark Bay tend to occur seasonally in the austral spring and summer (September through January) (Connor *et al.* 1996; Richards 1996), juveniles were grouped by birth cohorts, *e.g.*, a dolphin born in December 1986 was assigned to the 1986-87 birth cohort. Thus, dolphins were advanced as cohorts to the next year of age in September, the first month of the birth season in Shark Bay.

RESULTS

Sex difference in the association of juveniles with their mothers

Male juveniles rarely spent time with their mothers, whereas female juveniles were commonly found in the same social group as their mothers. Overall association coefficients of juvenile sons with their mothers were significantly lower than those of juvenile daughters (n=3 males, 6 females; Mann-Whitney U=24, p=0.012; Fig. 1). Specifically, overall association coefficients of female juveniles with their mothers ranged from 22 to 69, whereas those of male juveniles ranged from 0 to 11 (Table 2, Fig. 1). There was overlap in the annual association coefficients of only one male (Skini) and one

female (Yin) at age 7-8 yr (Table 2).

Overlap in ranging patterns of juveniles with their mothers

The ranging patterns of two juvenile males suggested that the low association coefficients of mothers with their juvenile sons could not be attributed to movement of young males away from the natal region. There was considerable overlap in the ranging patterns of each juvenile male with that of his mother (Fig. 2), suggesting that, although juvenile sons did not spend time in the social groups of their mothers, they nevertheless continued to live within the same general area.

There was also considerable overlap in the ranging patterns of each of two juvenile females with that of her mother, an expected result given that mothers and daughters were often sighted in each other's company.

Sex difference in top-ranked associates of juveniles

Preliminary results suggested that male and female juveniles may also differ in the age and sex of their top-ranked associates (Table 3). In particular, the top-ranked associates of each of three juvenile females were adult females (with and without calves) and other juvenile/subadult females. For two of the three juvenile females, her mother was a close associate. Association coefficients of the three top-ranked associates of these young females ranged from 43 to 69. For two juvenile females who were each other's closest associate, there was considerable overlap in their top-ranked associates.

The sample size for juvenile males was limited to a single individual. Top-ranked social associates of this juvenile male were entirely unlike those of his female counterparts: his most common associates were four known juvenile/ subadult males and one juvenile/subadult suspected to be male. Association coefficients of the three top-ranked associates of the male juvenile ranged from 46 to 50.

DISCUSSION

Female juvenile bottlenose dolphins continued to associate with their mothers for several years following weaning. Juvenile sons, on the other hand, rarely spent time with their mothers after independence, even though they apparently remained in the same general area. Richards' (1996) more detailed analysis of a subset of the data reported herein confirmed that there was no difference between sons and daughters in the degree of range overlap with the mother.

In addition to this sex difference in the association patterns of juveniles with their mothers, preliminary results suggested that the broader social network of juvenile males may be quite different from that of their female counterparts. One juvenile male had as his top-ranked associates several same-aged males, a social milieu resembling the male-biased, age-segregated "subadult groups" of juvenile males in Florida (Wells 1991).

In contrast, primary social associates of three juvenile females in Shark Bay included their mothers as well as other same-aged and adult females. The tendency of juvenile females in this study to preferentially associate with their mothers and other females indicates that the primary social setting for maturing Shark Bay females is likely to be within the network of adult females, rather than the subadult group suggested for Florida juvenile females (Wells 1991). While there may be real differences in the social lives of juvenile females in Florida and Western Australia, the many fundamental similarities in the social structures of these two populations (*e.g.*, Wells *et al.* 1987, Smolker *et al.* 1992) belie such an explanation. It is more likely that the two data sets complement each other such that Florida observations were biased towards juvenile males (Wells 1991) and Shark Bay observations towards juvenile females (Table 1). As a result, each study provides a more comprehensive picture of juveniles of the opposite sex.

Sex differences in association patterns of the juvenile dolphins of Shark Bay conform to broader mammalian patterns. Differences between the sexes in life histories and adult social behavior -- manifested in patterns of dispersal, group membership, parental behavior, mate acquisition, and/or attainment of social rank -- are often portended by the behavior of juvenile conspecifics. Many of the differences between male and female juvenile primates -- for example, in partner preferences, play, interactions with infants, grooming, and agonism -- correspond to differences in the behavior of adults of each sex (*e.g.*, reviewed in Pereira and Altmann 1985; Walters 1987). With respect to social relationships, juveniles are predicted to selectively invest in those long-term relationships likely to benefit them in the future (*e.g.*, Cheney 1978; Fairbanks 1993). Juvenile vervet monkeys seem to do just that: Fairbanks (1993) found that juvenile females -- destined to remain for life within their natal group -- developed long-lasting, affiliative relationships with their mothers and other adult females with whom they might associate as adults, but were less selective in their allocation of allomaternal care. In contrast, juvenile males -- who would disperse around puberty -- developed long-term relationships with similar-aged males with whom they might emigrate, but had brief associations with adult females during periods of sexual receptivity.

Thus, sex differences in the behavioral development of juvenile bottlenose dolphins might be expected on the basis of the many differences expressed by adult males and females of this species, including sexual dimorphism in adult body size (Read *et al.* 1993; Tolley *et al.* 1995), sexual bimaturism (Wells *et al.* 1987), and sex differences in ranging behavior (Wells *et al.* 1987) and competitive behavior (Samuels and Gifford, in press).

Sex differences in the social associates of juvenile dolphins appear to foreshadow their adult social networks. Although the evidence suggests that neither sex disperses (Wells *et al.* 1987; Wells 1991; Duffield and Wells 1991; Richards 1996), as adults,

bottlenose dolphins tend to be sexually segregated as a consequence of the close, preferential relationships between adults of the same sex (Wells *et al.* 1987; Smolker *et al.* 1992). The association of juvenile males primarily with other young males of similar age (Wells 1991; this study) is a likely precursor to development of the long-term, cohesive relationships among two or several adult males (Wells 1991). Juvenile females, on the other hand, appear to be part of a network of females including matrilineal kin (this study), a social milieu very much like that of adult females (Wells *et al.* 1987, Scott *et al.* 1990, Smolker *et al.* 1992).

It remains to be determined whether the behavior of juvenile dolphins is geared primarily towards current survival, towards acquiring skills and relationships that will contribute to future reproductive success, or both. As with primates and other mammals, we expect juvenile dolphins to engage in specific short-term relationships that enable them to practice skills necessary for future reproductive effort (*e.g.*, play-fighting for males; interactions with infants for females). Long-term study will resolve whether juvenile bottlenose dolphins also selectively cultivate relationships with certain individuals who will become social allies in the juveniles' adult lives.

Delving more deeply into the social development of juvenile dolphins will require development of a more-focused research methodology. Our current understanding of the social lives of juveniles is limited, in part, by the *ad libitum* nature of the data sets (Wells 1991; this study). The biases inherent in group-focused sighting records may be greatest for small, indistinctly-marked juveniles whose presence or activity is easy to overlook in a group of dolphins. In addition, a data set influenced by group visibility may be biased towards groups that tend to be animated (*e.g.*, juvenile males in subadult groups) over those that are relatively calm (*e.g.*, juvenile females in female bands). In the present study, the opposite appeared to occur: collection of sighting records in the primary context of searching for focal adult females may have skewed the sample towards female juveniles and resulted in poorer representation of juvenile males.

For these reasons and more, we suggest that a fuller understanding of the social lives of juvenile dolphins will result from use of behavioral sampling techniques that are designed to minimize the biases introduced by sex- and age-related differences in behavior (Altmann 1974). Specifically, using focal-animal sampling techniques, behavioral studies of juvenile dolphins of known age, known sex, and known matrilineal group will determine how and when members of this life stage develop the social relationships that will be important in their adult lives.

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Table 1. Juvenile dolphins of Shark Bay during 1990-1993 listed by sex in decreasing age order.

Sex	Juvenile	Mother	Birth cohort	Age Range (yr)
♀	Zag	Zig	≤1983-84[1]	8-9
	Flip	Blip	≤1983-84[2]	7-9
	Squarelet	Square	1984-85	6-8
	Yin	Yan	1984-85	6-8
	Demi	Halfluke	1986-87	5-6
	Zippy	Zig	1986-87	4-6
♂	Skini	Mini	≤1983-84[2]	7-9
	Booboo[3]	Yogi	≤1983-84[2]	7-8
	Seebe	Eed	1986-87	4-6

[1] First observed as a dependent calf in 1984-85. Presumed born in previous birth season (1983-84) or even earlier, due to her large size at first sighting. Based on analysis of mother-calf association patterns, presumed independent by 1985-86 (Richards 1996).

[2] First observed as dependent calves in 1984-85. Presumed born in previous birth season (1983-84); presumed to be younger than Zag because of smaller size at first sighting. Based on analyses of mother-calf association patterns, Flip and Booboo presumed independent by 1987-88 and Skini by 1988-89 (Richards 1996).

[3] Orphaned when mother disappeared/died in 1992; not included in 1992-93 analyses.

Table 2: Association coefficients of juveniles with their mothers during 1990-1993 (see text for explanation). Juveniles are listed by sex in decreasing age order.

Sex	Juvenile	n[1]	Annual Coefficient						Overall Coefficient
			Age (yr): 4	5	6	7	8	9	
♀	Zag	46					30	46	35
	Flip	60				24	33	45	37
	Squarelet	259			73	68	66		69
	Yin	89			37	0	11		22
	Demi	13		40	50				46
	Zippy	72	52	40	46				47
♂	Skini	56				14	0	10	11
	Booboo	39				0	0		0
	Seebe	27	0	0	0				0

[1] Total number of association sightings of juvenile and mother.

Table 3: Top-ranked associates of selected juveniles based on survey records from 1990-93 (see text for explanation).

Juvenile (age)	Associates			
	Overall Coefficient	Sex	Age Class	Name and Kinship (if known)
♂ Skini (7-9 yr)	50	♂	juv/subad[1]	Ridges
	47	♂	juv/subad	Prima
	46	♂	juv/subad	Natag
	38	probable ♂	juv/subad	Pong
	29	♂	juv/subad	Big
♀ Flip (7-9 yr)	59	♀	juvenile	Zippy
	45	♀	adult	Scratches
	43	♀	adult w/calf	Zippy's mother
	42	♀	juvenile	Zippy's sister
	39	♀	adult w/calf	Uhf
♀ Squarelet (6-8 yr)	69	♀	adult w/calf	Squarelet's mother
	63	♀	adult	Tweedledee
	56	♀	adult	Fatfin
	23	♀	adult w/calf	Uhf
	21	♀	juv/subad	Lick
♀ Zippy (4-6 yr)	59	♀	juvenile	Flip
	56	♀	juvenile	Zippy's sister
	49	♀	adult w/calf	Zippy's mother
	40	♀	adult w/calf	Uhf
	29	♀	adult	Scratches

[1] "juvenile/subadult"

Figure 1: Sex difference in the association of juvenile dolphins with their mothers. Overall association coefficients (from Table 2) are plotted for male and female juveniles.

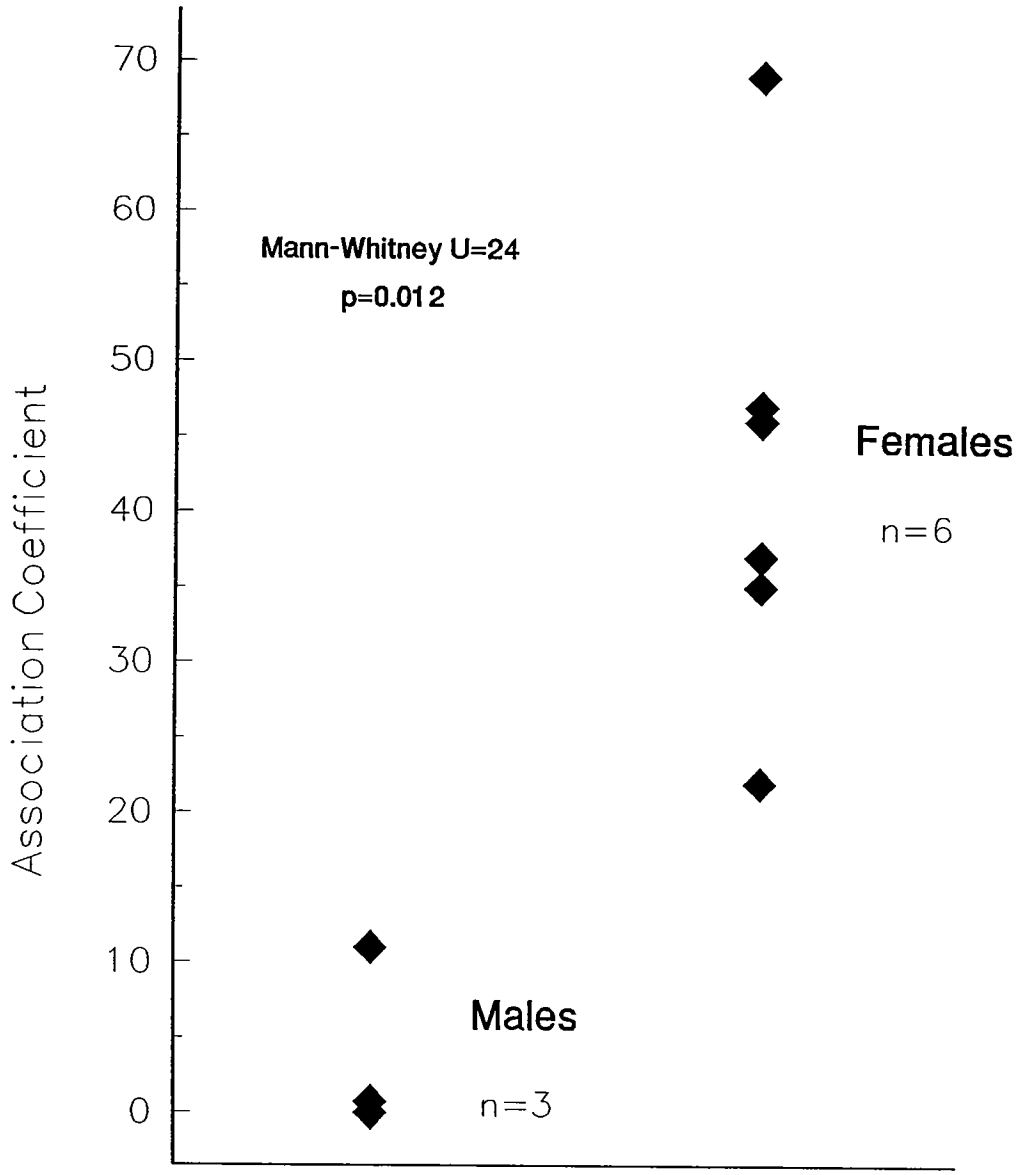

Association Coefficient
70
60
50
40
30
20
10
0
Mann-Whitney U=24
p=0.012
Females
n=6
Males
n=3

Figure 2: Ranging patterns of two juvenile males compared with that of each one's mother (see text for explanation). (a) juvenile male Skini

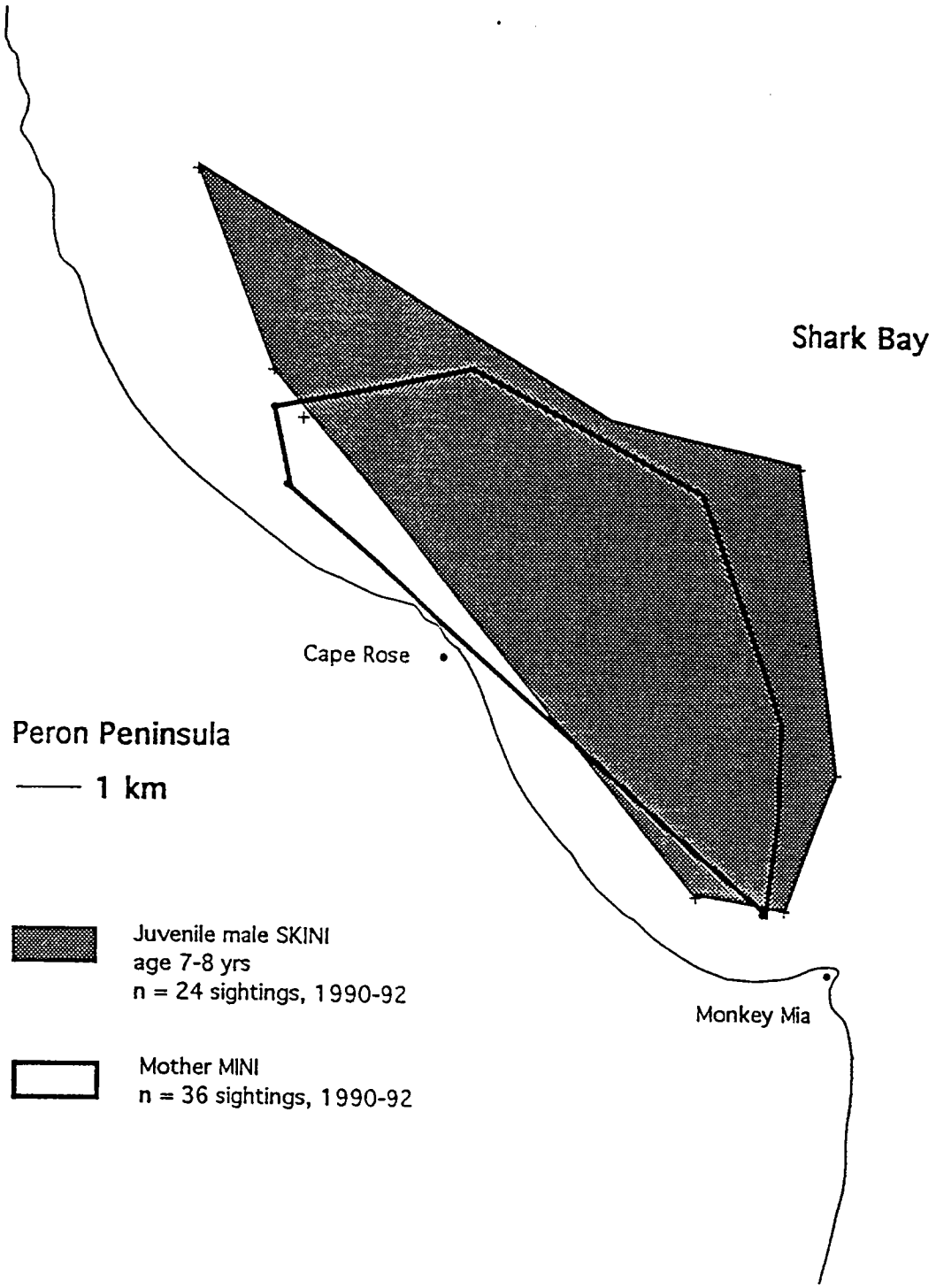
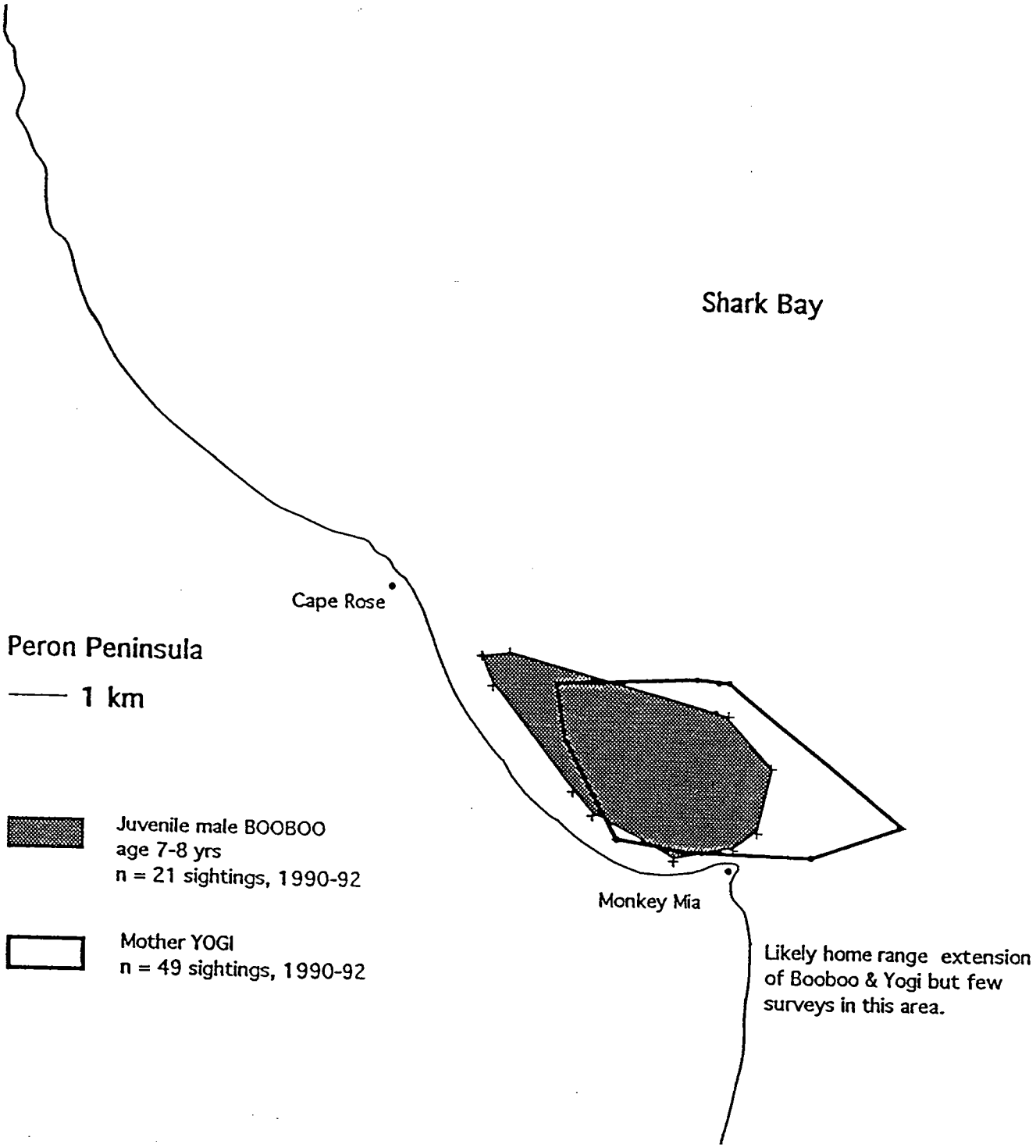

Shark Bay
Cape Rose
Peron Peninsula
1 km
Juvenile male SKINI
age 7-8 yrs
n = 24 sightings, 1990-92
Mother MINI
n = 36 sightings, 1990-92
Monkey Mia

Figure 2: (b) juvenile male Booboo


Shark Bay
Cape Rose
Peron Peninsula
1 km
Juvenile male BOOBOO
age 7-8 yrs
n = 21 sightings, 1990-92
Mother YOGI
n = 49 sightings, 1990-92
Monkey Mia
Likely home range extension
of Booboo & Yogi but few
surveys in this area.

CHAPTER 4.

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QUANTITATIVE BEHAVIORAL STUDY OF BOTTLENOSE DOLPHINS IN SWIM-WITH-DOLPHIN PROGRAMS IN THE UNITED STATES

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ABSTRACT

The behavior of dolphins in four Swim-With-Dolphin programs was compared by type of Swim encounter, defined by the presence ("Controlled") or absence ("Not-Controlled") of explicit trainer regulation of interactions between dolphins and human swimmers. Dolphin-swimmer interactions involving aggressive, submissive, or sexual behavior were designated as "high-risk" in the Swim context; sexual behavior was included as high-risk based on analyses that demonstrated co-occurrence of sexual and agonistic behaviors. High-risk activity comprised a substantial proportion of dolphin-swimmer social activity during Not-Controlled Swims. In contrast, high-risk activity rarely occurred during Controlled Swims, even though agonistic and sexual behaviors were normal components of the same dolphins' free-time social repertoire. These results indicated that direct trainer control of dolphin-swimmer interactions virtually eliminated high-risk activity from the Swim context, and thereby diminished the potential for dolphin distress, swimmer injury, and rejection of dolphins from Swim programs due to swimmer injury. This study illustrates effective use of quantitative behavioral sampling techniques for evaluation of captive management concerns and promotes broader use of these techniques for a better understanding of cetacean behavior.

Key words: bottlenose dolphin, social behavior, human-dolphin interactions, swim-with-dolphin.

Swim-With-Dolphin programs allow members of the public to enter a pool with one or more captive dolphins for recreational swimming. The National Marine Fisheries Service (NMFS) first authorized use of bottlenose dolphins (*Tursiops truncatus*) in a Swim program in 1985, and three additional programs were permitted in 1987–1988. These four programs operated under experimental, provisional public display permits for the next five years, pending

determination by NMFS whether such programs adversely affected the health and well-being of dolphins. An extensive review of Swim program issues and concerns (NMFS 1990) revealed insufficient data to make definitive conclusions about effects of these programs on dolphin behavior. Because it was not known whether dolphins in Swim programs exhibited unusual aggression, aberrant behavior, or behavioral signs of stress, the present study of bottlenose dolphins participating in Swims was designed as the behavioral component of an empirical evaluation of these programs by NMFS (Samuels and Spradlin 1994).

The quantitative sampling techniques for this study were adapted from methods developed in the course of extensive behavioral research on bottlenose dolphins at Brookfield Zoo (Samuels *et al.* 1989, 1991), which in turn had been adapted from procedures widely used in behavioral research on terrestrial animals (Altmann 1974). Further refinement of the protocol to document interactions of dolphins with human swimmers was based on recommendations generated at workshops that were convened by the Marine Mammal Commission in 1990 (Wells and Montgomery 1990) and by NMFS in 1992. An important outcome of the NMFS workshop was that the participants, including operators of the original four Swim programs, NMFS representatives, and the authors, reached general consensus on behaviors-of-concern in the Swim context.

Specific goals of the present study included: (1) to identify and quantify the frequency of specific dolphin activities that occur in the Swim context, (2) to evaluate short-term effects of Swim participation on dolphin behavior by using the dolphins as their own controls and comparing their behavior during Swims with their "normal" behavioral profiles during free time, (3) to identify and quantify the frequency of Swim activities that pose risk to dolphins or human swimmers, (4) to identify classes of dolphins or swimmers that are disproportionately involved in risky activity, and (5) to evaluate suitability of refuge-area types based on usage by dolphins.

Methods

Study Schedule

A pilot study was conducted from August 1992 to March 1993 to develop guidelines for the formal study, specifically to (1) identify a basis for comparison among Swim programs, (2) develop an identical sampling protocol for all four Swim programs that provided unbiased records of dolphin behavior, (3) design an observation schedule that ensured adequate sample sizes, and (4) refine the list of behaviors-of-interest compiled at the 1992 NMFS workshop. The pilot study included observer training in behavioral sampling techniques at Brookfield Zoo for one month and observations at the four Swim programs for two months. Pilot study data were not comparable from all programs because the preliminary protocol was modified several times and observer proficiency improved. Consequently, pilot study data were not included in this report.

The formal study was carried out in two phases during May–June and October–December 1993. During each study phase observations were conducted

at each of the four Swim programs: Dolphin Quest, Waikoloa HI; Dolphin Research Center, Marathon Shores FL; Dolphins Plus, Key Largo FL; and Theater of the Sea, Islamorada FL.

Basis for Comparison of Swim Programs

Dolphin behavior was compared between types of Swim encounters that were defined by the level of direct trainer control of dolphins and swimmers. We defined two Swim types based on the presence ("Controlled") or absence ("Not-Controlled") of explicit trainer regulation of dolphin-swimmer social interactions. Controlled Swims were offered at Dolphin Quest, Dolphin Research Center, and Theater of the Sea; Not-Controlled Swims were offered at Dolphins Plus and Theater of the Sea. Hereafter in this report, programs are identified by arbitrary labels (1 to 4) or by Swim type, instead of using facility names.

Controlled Swims—Trainers had direct control over the movements and interactions of dolphins and swimmers, *i.e.*, trainers determined when interactions would occur, which dolphins and swimmers would take part in interactions, what kinds of interactions would occur, and what the duration of interactions would be. Typically, dolphins were positively reinforced with fish for performing specific trained behaviors, and dolphins and swimmers were separated when not engaged in trainer-controlled interactions to preclude spontaneous socializing. Although, in one program, positive food reinforcement was not always linked to specific trained behaviors, this was considered to be a Controlled format because trainers directly controlled swimmer movements and dolphin-swimmer interactions.

Not-Controlled Swims—Staff watched over but did not explicitly direct the movements or interactions of dolphins and swimmers. Swim participants (dolphins or swimmers), and not staff, were the ones who determined which dolphins and swimmers would interact, when interactions would occur, what kinds of interactions would occur, and what the duration of interactions would be. Although specific dolphin-swimmer interactions were not directly controlled by staff, these Swims were supervised in several ways. In one program dolphins were periodically recalled by a trainer and given positive food reinforcement; however, this was considered to be a Not-Controlled format because trainers did not direct specific dolphin-swimmer interactions. In the other program, staff advised swimmers about aspects of their behavior but did not direct specific dolphin-swimmer interactions or use positive reinforcement to shape dolphin behavior.

In one program, the first half of each Swim session was Controlled and the second half was Not-Controlled. These observations were especially valuable for comparing dolphin behavior between Swim types because, within each Swim session, the same dolphins participated in Controlled and Not-Controlled formats with the same swimmers under supervision of the same training staff in the same pool. Thus, in this program, differences in dolphin behavior between Controlled and Not-Controlled formats were likely to be attributed to the

Table 1. Total number of dolphins authorized to participate in Swim programs (NMFS, unpublished) *vs.* number observed during this study (in parentheses). Footnotes explain discrepancies.

Program	Total dolphins	Adult and maturing ♂♂	Adult and maturing ♀♀	All immatures
1	7 (6)	—	4 (1–4[b,c])	3 (2[a])
2	6 (6)	2 (1–2[c])	4 (4)	—
3	3 (2)	2 (1[d])	1 (1)	—
4	12 (8)	2 (0–1[c,d])	10 (6–7[b,c,d])	—
Total	28 (22)	6 (3–4)	19 (12–16)	3 (2)

[a] The sole dependent calf in the Swim population was not a subject of this study (see text for explanation).

[b] Temporary removal from Swims for calving: 2 adult females.

[c] Temporary removal from Swims for other management reasons (*e.g.*, mating, behavior, unspecified): 2 adult males, 2 maturing females, 2 adult females.

[d] No participation in Swims due to long-term removals for other management reasons (*e.g.*, mating, behavior, unspecified): 2 adult males, 1 adult female.

presence or absence of direct trainer control and not to any other feature of the program.

Dolphins Participating in Swims

There were 28 dolphins authorized to participate in Swims during the study period (Table 1; NMFS, unpublished). Two-thirds of these dolphins were adult and maturing females; 21% were adult and maturing males; and 11% were immature, *i.e.*, < 8 yr old and pre-reproductive (Table 1).

All Swim dolphins were potential subjects of this study, with one exception—a calf was not a subject because he was the sole infant among Swim dolphins, and pilot study data indicated that his movements were highly correlated with those of his mother. Of 27 potential subjects, 22 dolphins participated in Swims during the study period and were, therefore, subjects of this study (Table 1). Variation in dolphin participation, and consequently in observation time per dolphin, resulted from short- and long-term removals by staff due to mating, calving, unusual behavior, or other events (Table 1). Adult and maturing males were particularly underrepresented as study subjects because half of these males did not participate or participated at low levels in Swims during the study (Table 1).

Human Swimmers Participating in Swims

A total of 1,282 human swimmers participated in Swims that were observed during the study (Table 2). Swimmer age/sex classes were used in recording details of dolphin interactions with swimmers. Classes of swimmers were visually assessed by observers, using the following age categories: (1) child (prepubescent),

Table 2. Human swimmers participating in Swims observed during the study, listed in order of age/sex class prevalence.

Program	Total swimmers	Adult ♀	Adult ♂	Teen ♀	Teen ♂	All children	All seniors
1	204	62%	28%	2%	0%	5%	2.5%
2	446	53%	25%	14%	6.5%	1%	<0.3%
3	92	47%	31.5%	12%	6.5%	2%	1%
4	540	48%	34%	6%	3%	9%	<0.4%

(2) teenager (pubescent), (3) adult, and (4) senior (approximately 60+ yr old). In all programs swimmers were predominantly adult women; the second most common class was adult men (Table 2). Participation of children was allowed in two programs; few seniors participated in any program (Table 2). Mean number of swimmers per Swim session generally conformed to the maximum 2-swimmers-per-dolphin ratio mandated by NMFS (1990, p.74), *i.e.*, 3.8 swimmers per 1–2 dolphins in Program 1; 6.0 swimmers per 2–4 dolphins in Program 2; 3.8 swimmers per 2 dolphins in Program 3; and 7.1 swimmers per 4–8 dolphins in Program 4.

Quantitative Behavioral Sampling Techniques

A detailed description of behavioral sampling methods is provided in Samuels and Spradlin (1994). Behavioral sampling was based on a focal-animal sampling scheme (Altmann 1974) in which the activities, associates, and social interactions of a single dolphin were the focus of each observation period. Selection of subjects for daily observations was predetermined by the observers to promote equal, unbiased coverage of all dolphins. Observations were conducted during dolphins' two primary daytime activities: Swim sessions with members of the public (107 h, Table 3) and free time in which neither swimmers nor trainers interacted with dolphins (94 h, Table 3).

Table 3. Observations conducted per program and per observation type.

		Swims			Free time		
Program	Total days	Periods	Hours	Median h/ dolphin	Periods	Hours	Median h/ dolphin
1	33	58	17.1	2.95	54	25.3	4.05
2	22	74	35.1	6.1	76	24.3	4.6
3	10	24	12.2	6.15	24	11.8	5.9
4	28	76	42.7	6.1	71	32.4	4.65
Total	82[a]	232	107.1		225	93.8	

[a] The total number of observation days did not equal the sum of days spent at each program because on several occasions we conducted observations at two programs on the same day.

Table 4. Categorization of social interactions of dolphins with swimmers or dolphins.

Category	Behaviors
Aggressive	[a] bite, body-slam, forceful push (*e.g.*, into structure, away from dock, underwater), ram, threat (head-jerk, jawclap, open-mouth); [a,b] chase, hit
Submissive	[a] flee; [a,b] flinch; [b] scream (*e.g.*, "ouch!")
Sexual	[a] beak-to-genital propulsion, erection, genital insertion, mount, repetitive genital rubbing, thrust
Abrupt	[a] breach, chuff, leap, propoise, quick-swim, rapid circling, white-water; [a,b] abrupt-turn, quick-approach, slap-water, any spontaneous behavior performed abruptly; [b] grab
Neutral/affiliative	[a,b] all gentle touching (*e.g.*, gentle push, gentle rub), object-manipulate, rest-together, swim-together, all other trained behaviors (*e.g.*, foot-push, kiss, mimicry); [b] hold, reach

[a] Performed by dolphins to swimmers and by dolphins to other dolphins.
[b] Performed by swimmers to dolphins.

Differences in observation time per program and per dolphin (Table 3) were dictated by program differences in the durations of Swim sessions, the number of scheduled Swim sessions per day, and the number of participating dolphins. We focussed on the behavior of a single dolphin per Swim session, and individual dolphins were typically observed no more than once per observation condition per day (except at Program 3 where two dolphins participated in three daily Swims). The scheduled duration of Swim sessions per program dictated the length of our observation periods; mean durations ranged from 17.7 min (Program 1) to 33.7 min (Program 4). The duration of free-time observation periods was 30 min; however, because free time was sometimes interrupted, mean durations of free-time observation periods ranged from 19.2 min (Program 2) to 29.5 min (Program 3).

Behavioral information about the focal dolphin was recorded primarily using instantaneous sampling techniques (Altmann 1974), *i.e.*, point samples recorded every 30 sec. Brief, rare interactions may be missed by this technique, but the 30-sec interval minimized such data loss. During Swims, each point sample contained the following information about the focal dolphin: (1) identity of dolphin(s) within 1 m, (2) age/sex class of swimmer(s) within 1 m, (3) location (within designated refuge area or not), (4) behavioral state (defined below), (5) details of social interactions with swimmers or other dolphins, and (6) general conditions that might influence dolphin behavior. During free time, each point sample contained the same information except proximity to swimmers.

Behavioral states were defined to distinguish between activities that were social *vs.* non-social, and under direct trainer control (on-command, trained) *vs.* not under direct trainer control (not on-command, spontaneous). Trainer-controlled activities were further distinguished by correct or incorrect execution of on-command trained behaviors, a distinction based primarily on trainer com-

Table 5. Number of point samples that were the basis for estimates of proportion of time dolphins spent in specified activities[a]. Analyses are: (A) Swim profiles; (B) high-risk and abrupt activity; (C) behavior during Swims *vs.* free time; and (D) refuge usage.

Observation condition	Analysis	Type of "time"	Program:	Controlled 1	Controlled 2	Controlled 3	Not-controlled 3	Not-controlled 4
Swim	A, D[b]	In-water		1,755	2,910	600	593	4,302
	C	All social		430	1,050	139	151	2,143
	B	Dolphin-swimmer social		424	984	137	140	686
Free	D	All free		2,839	2,805	—— 1,402 ——		3,731
	C	All social		1,243	1,229	—— 136 ——		1,373

[a] Because point samples were recorded every 30 sec, dividing the number of point samples by 2 provides an estimate of number of observation min (not including point samples that were unknown).

[b] Instances in which trainer-commanded behavior resulted in dolphins entering the designated refuge were omitted from this analysis (n = 82 point samples omitted).

mentary. Six mutually-exclusive behavioral states of the focal dolphin were recorded using a standardized coding scheme: (1) trained social interactions executed correctly, or (2) incorrectly; (3) trained non-social behaviors executed correctly, or (4) incorrectly; (5) spontaneous social interactions; and (6) spontaneous non-social behaviors.

Social interactions were defined as one or more behaviors listed in Table 4 performed without interruption by the focal dolphin with one or more partners (swimmer or dolphin) who were within 1 m and whose identity was constant. Detailed descriptions of social interactions of the focal dolphin were recorded using a standardized coding scheme and included (1) all behavioral components, (2) directionality of behaviors, and (3) identities of initiator(s) and recipient(s). All social behaviors were defined precisely (Samuels and Spradlin 1994).

General conditions were defined to partition point sample data according to swimmer or trainer activities likely to influence dolphin behavior. During Swim observations, general conditions referred to swimmer opportunities for interactions with the focal dolphin: (1) limited opportunities *i.e.*, swimmers were separated from dolphins on steps or on beach; (2) partial-immersion opportunities *i.e.*, swimmers were sitting on a dock; (3) full, "in-water" opportunities *i.e.*, swimmers were standing in shallow water, hanging onto a dock, or swimming; and (4) temporarily interrupted opportunities *i.e.*, any unscheduled divergence from normal Swim procedures dictated by trainers and/or any unscheduled departure from Swims by one or more swimmers. During free-time observations, general conditions referred to the presence or absence of trainer activities near the focal dolphin's pool.

Two other sampling regimes were employed simultaneously with point sampling. Continuous (all-occurrence) sampling (Altmann 1974) of social interac-

tions of focal dolphins was conducted during Swims, and *ad libitum* (opportunistic) sampling (Altmann 1974) of unusual events and social interactions involving non-focal dolphins was conducted during Swims and free time. All-occurrence data were used only to evaluate co-occurrence of certain behavioral categories (see "High-risk activity" below); anecdotal *ad lib* data were used only to clarify aspects of the quantitative dataset. The same definitions and recording rules described for point sampling were used to record all-occurrence and *ad lib* social interactions.

Modifications for Difficult Observation Conditions

Problems inherent in observing marine animals from above water were further exacerbated by difficult observation conditions at all four facilities, *e.g.*, murky water, large pool size, and/or surface glare. A single observer was unable to track the focal dolphin and record consistently the desired information; thus, all data collection was conducted by two observers (C. Pelton, T. Spradlin) who worked together as a team.

A point sample was scored as "unknown" if, at the sound of a 30-sec-interval beeper, the focal dolphin was out of sight and did not reappear within 10 sec. Viewing was somewhat limited (*i.e.*, 3%–6% of point samples were unknown) during observations of (1) Not-Controlled Swims (in which dolphin and swimmer movements were not restricted to the surface) at one program, and (2) free time (in which dolphins spent considerable time underwater) at two programs. However, observers were able to record nearly all point samples (< 1% unknown) during observations of: (1) all Controlled Swims (in which dolphin and swimmer movements were restricted to the surface) at three programs, (2) Not-Controlled Swims and free time at one program (where only two dolphins were present), and (3) free time at one program (where the water was clear).

Data Analyses

Analyses in this report were based on all free-time data and a subset of Swim data collected when swimmers had full, in-water opportunity to interact with dolphins (Table 5). Although interactions with dolphins occurred in other contexts, we reported only in-water data because swimmer immersion is what distinguishes Swims from other types of interactive encounters with the public, *e.g.*, petting pools. In-water data were combined regardless of swimmer location, *i.e.*, swimmers were swimming (all programs), holding onto a dock (three programs), or standing in shallow water (one program). The proportion of each Swim session that was in-water differed by program, ranging from 70% in Program 2 to 92% in Program 4.

To facilitate data tabulation, behavioral data were entered into a database program (Paradox 1992). Analyses were carried out using computerized statistical programs (SAS Institute Inc. 1985, SYSTAT 1992), and results were plotted using a computerized graphics program (Axum 1992).

Classification of Social Behavior

Social behavior was classified into five broad categories on the basis of key components (Table 4). We used standard classes of behavior relevant to dolphin-dolphin and dolphin-swimmer interactions (*i.e.*, aggression, submission, sexual, neutral/affiliative), and we created a fifth category, "abrupt", that included behaviors suggested in the literature, but not yet demonstrated, to be aggressive (*e.g.*, slap-water, quick-approach).

High-risk activity—Dolphin-swimmer social interactions were considered to be "high-risk" when one or more behavioral components posed risk for one or both participants in the Swim context. We identified three behavioral categories as high-risk: (1) aggression, (2) submission, and (3) sexual behavior.

Risk was clearly posed in interactions that were agonistic, *i.e.*, involved aggressive and/or submissive behaviors. Aggression is typically characterized by threats or forceful attempts to inflict harm (Table 4). Submission is typically characterized by behaviors associated with avoidance, withdrawal, escape (flee, flinch) or fear (scream). Because submissive behaviors are incompletely described for cetaceans, we provide more detail here. In the present study submissive behavior was defined as an immediate response to the action of another individual. "Flee" was defined as a rapid departure from another to a distance of > 1 m; "flinch", which was first described as the cetacean equivalent of the primate "cower" (Samuels and Gifford, in preparation), was similarly defined in the present study as cringing or jerking away from another. These behaviors have been traditionally used as indicators of submission in studies of primates (*e.g.*, Hausfater 1975) and were recently identified as important indicators of dominance relationships among bottlenose dolphins (Samuels *et al.* 1991, Samuels and Gifford, in preparation).

Sexual behavior (Table 4) was added to the high-risk category (*cf.*, NMFS 1990, Wells and Montgomery 1990) subsequent to analysis of data from Not-Controlled Program 4, the only program in which dolphins and swimmers engaged in such behavior. We analyzed a subset of data (20 h, 31 Swim sessions) collected during the second phase of the study when six female dolphins participated in Swims. In this analysis, we used all-occurrence data because this dataset provided an exact count of all interactions involving agonistic and/or sexual components. The data were partitioned into 3-min intervals, and each interval was categorized by the number of interactions involving agonistic and/or sexual behaviors of the focal dolphin with swimmers. A 3×4 matrix contained the number of 3-min intervals in which 0, 1, or 2+ interactions included agonistic behaviors and 0, 1, 2, or 3+ interactions included sexual behaviors. Using the Mantel-Haenszel Chi-square test (Mantel and Haenszel 1959, SAS Institute Inc. 1985), we found a significant linear co-occurrence of sexual and agonistic interactions—the number of interactions involving agonistic behavior increased with the number of interactions involving sexual behavior per 3 min of observation (Mantel-Haenszel Chi-square = 53.9, df = 1, $P < 0.001$; $n = 636$ interactions during 406 3-min intervals; Fig. 1).

Abrupt activity—Although not demonstrated to be antagonistic, abrupt

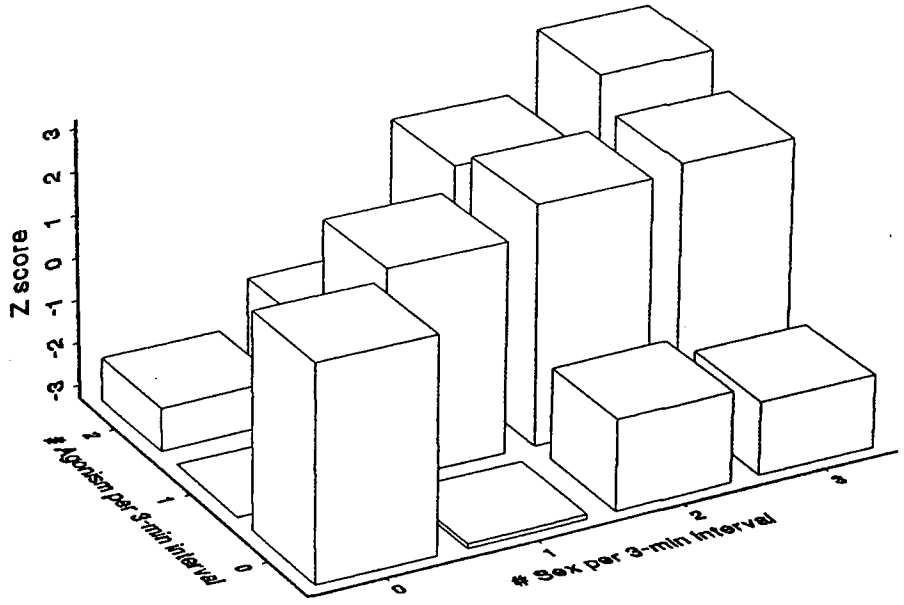

Figure 1. Co-occurrence of sexual and agonistic behavior in encounters between dolphins and swimmers in one Not-Controlled program. Cells correspond to the number of interactions per 3-min interval that were sexual (x-axis) and agonistic (y-axis); each bar represents the deviation from expected value per cell, expressed as a Z score (z-axis).

activity posed risk through forceful execution. We evaluated abrupt activity separately from high-risk activity.

Proportion of Time Spent in Specified Activities

Point sample data were used to estimate the proportion of time dolphins spent in specified activities (Table 5). For example, calculations of the proportion of time dolphins were involved in high-risk activity were based on dolphin-swimmer social time, *i.e.*, the number of point samples that were high-risk divided by the total number of point samples in which focal dolphins were involved in social interactions with swimmers.

In analysis of the proportion of dolphin-swimmer social time that was spent in high-risk or abrupt activity, each point sample of a dolphin-swimmer social interaction was classified by behavior category (Table 4). Categorization was hierarchical in approximate order of risk: (1) aggressive, (2) submissive, (3) sexual, (4) abrupt, and (5) neutral/affiliative. Thus, an interaction was included within a category if it contained one or more behavioral elements of that category and no components of categories higher on the list (Table 4). This hierarchical scheme resulted in, for example, some interactions classified as "aggressive" that also included submissive components.

In analysis of refuge usage by dolphins, we evaluated the proportion of time

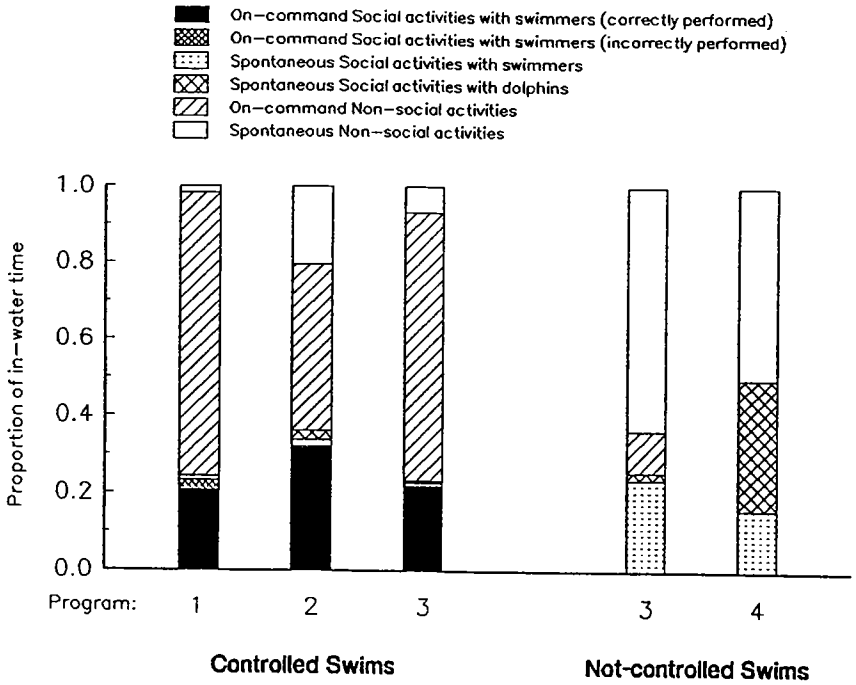

Figure 2. Proportion of in-water time during Controlled and Not-Controlled Swims that dolphins were engaged in social/non-social and on-command/spontaneous activities with swimmers, other dolphins, or alone.

spent in designated refuge areas during Swims and free time. Free time spent in the refuge area was used as a measure of the dolphins' ability to freely and voluntarily enter this space. For Controlled Swims, we also evaluated time spent to be in effective refuge when they were beyond swimmer reach (>1 m) and not under direct trainer control.

Results

Profile of Swim Sessions

Profile of dolphin activity—During Controlled Swims, the most common dolphin activities were performance of trained behaviors that were watched by swimmers ("on-command non-social" in Figure 2), and socializing with swimmers under direct trainer control ("on-command social with swimmers" in Figure 2). During Controlled Swims, dolphins rarely engaged in social interactions with swimmers that were not under direct trainer control ("spontaneous social with swimmers" in Figure 2) nor did they engage in social interactions with other dolphins ("spontaneous social with dolphins" in Figure 2).

During Not-Controlled Swims, the most common dolphin activity was solitary non-social behavior that was not directed towards swimmers or other dolphins ("spontaneous non-social" in Figure 2). The second most common dolphin

activity was spontaneous socializing with swimmers in one program ("spontaneous social with swimmers" in Figure 2), and in the other program, socializing with other dolphins ("spontaneous social with dolphins" in Figure 2).

Profile of direct trainer control of dolphin-swimmer social activity—Following the definitions of Swim types, social interactions with swimmers that were under direct trainer control ("on-command social with swimmers" in Figure 2) occurred only during Controlled Swims and never during Not-Controlled Swims. In one Not-Controlled program dolphins were under direct trainer control during 11% of in-water time (Fig. 2); however, such trainer control consisted entirely of on-command behaviors that were not social (*e.g.*, stationing at dock).

During Controlled Swims, a high proportion of trainer-controlled dolphin-swimmer social activity was performed correctly, ranging from 86% in Program 1 to 96% in Program 3 (Fig. 2). The remainder of dolphin-swimmer social activity, which may be considered "mistakes" in the Controlled context, took two forms: incorrect execution of trained behaviors, or spontaneous social interactions occurring outside of trainer control.

Occurrence of Risky Activity During Swims

High-risk and abrupt activity between dolphins and swimmers—High-risk activity was a striking component of Not-Controlled Swims, comprising 9% and 61% of dolphin-swimmer social time in Programs 3 and 4, respectively (Fig. 3). In contrast, high-risk activity comprised ≤ 1% of dolphin-swimmer social time in each of the three Controlled programs (Fig. 3).

Abrupt activity occurred at a substantial rate only in one Not-Controlled program. When combined with high-risk activity, the proportion of dolphin-swimmer social time that was risky increased from 9% to 16% in Program 3. Addition of abrupt activity did not change risk profiles in other programs.

Who was at risk: dolphins or swimmers?—High-risk activity comprised a notable portion of dolphin-swimmer social time in Not-Controlled Swims; however, high-risk activity differed between programs with respect to which types of behavior predominated and which partner (dolphin or swimmer) was at risk. In one Not-Controlled program, aggressive and sexual interactions comprised 98% of high-risk activity (Fig. 3), and all aggressive and sexual behaviors were performed by dolphins and directed towards swimmers. In the other Not-Controlled program, submissive interactions comprised 100% of high-risk activity (Fig. 3), and all submissive behaviors were performed by dolphins in response to swimmer actions that were not overtly aggressive. These activities put swimmers at risk in the former program and dolphins at risk in the latter program.

During Controlled Swims, the small proportion of dolphin-swimmer social time that was high-risk was predominantly dolphin submission in response to non-aggressive swimmer actions (88% high-risk activity, Fig. 3).

Which swimmers were involved in high-risk activity?—The classes of swimmers involved in swimmer-at-risk interactions were evaluated with data from Not-Controlled Program 4 (where nearly all such interactions occurred). The

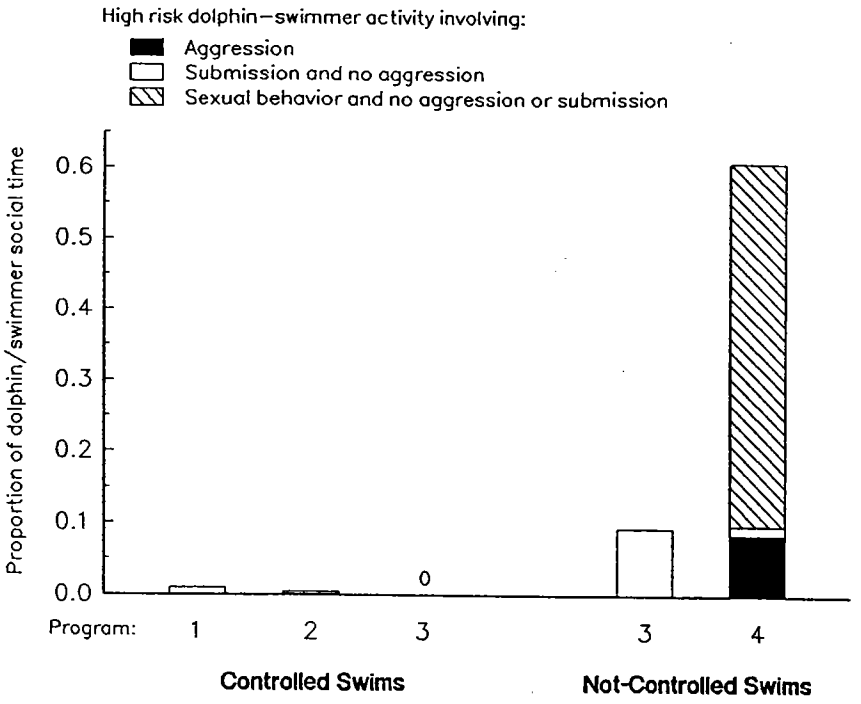

Figure 3. Proportion of dolphin-swimmer social time during Controlled and Not-Controlled Swims that dolphins were involved in high-risk activity with swimmers.

distribution of swimmers involved in swimmer-at-risk interactions differed significantly from the distribution of the full swimmer population in that program (Kolmogorov-Smirnov, 2-sample test, $P < 0.009$). In particular, Figure 4a shows that women and children were involved in swimmer-at-risk interactions disproportionately more often, and men disproportionately less often, than predicted by the distribution of age/sex classes in the full swimmer population.

The classes of swimmers involved in dolphin-at-risk interactions were evaluated across all Swim programs. The distribution of swimmers involved in dolphin-at-risk interactions differed significantly from the distribution of the entire swimmer population (Kolmogorov-Smirnov, 2-sample test, $P < 0.001$). In particular, Figure 4b shows that men were involved in dolphin-at-risk interactions disproportionately more often, and children and teens disproportionately less often, than predicted by the distribution of age/sex classes of the entire swimmer population.

Which dolphins were involved in high-risk activity?—This study did not identify, on the basis of observed behavior, classes of dolphins that were disproportionately involved in high-risk activity. Although nearly all dolphins involved in high-risk activity were adult and maturing females, this class constituted the majority of dolphins participating in Swims during the study, and therefore, the majority of observation time. Specifically, the 70% of dolphin-at-risk interactions involving adult or maturing female dolphins was proportionate

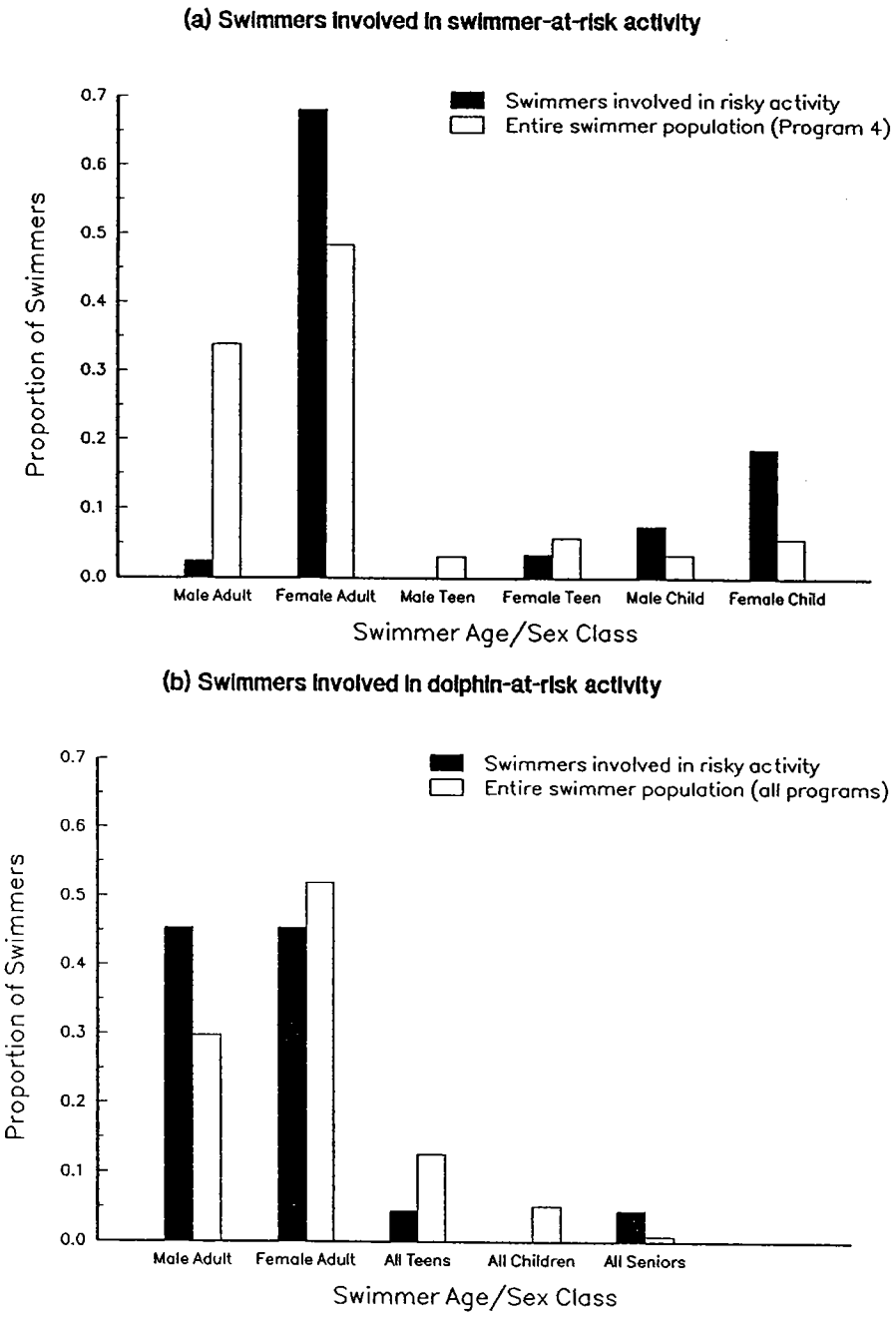

Figure 4. The distribution of swimmer age/sex classes (a) in Program 4 that were involved in swimmer-at-risk activity (n = 412 swimmer-at-risk point samples) compared with overall distribution of the swimmer population (n = 538 swimmers) (Fig. 4a), or (b) in all four programs that were involved in dolphin-at-risk activity (n = 22 dolphin-at-risk point samples) compared with overall distribution of the swimmer population (n = 1,282 swimmers) (Fig. 4b).

Table 6. Status of dolphins participating in Swims since inception of these programs (NMFS, unpublished).

Dolphin status	♂♂	♀♀
Long-term removal following injury to swimmer	3	0
Long-term removal for another reason	3	11
No long-term removal	6	16
Total	12	27

to the 73% of observation hours in which the focal was an adult or maturing female. Similarly, 100% of swimmer-at-risk interactions and 94% of observation hours were attributed to adult and maturing female dolphins (at Program 4 where nearly all such interactions occurred).

Records of dolphin participation in Swims since inception of these programs (NMFS, unpublished) provided a means of investigating what long-term consequences of high-risk activity might be for dolphins. NMFS's records indicated that long-term removal from Swim programs of male dolphins, but not females, has occurred in association with swimmer injuries as serious as broken bones. Specifically, there was a significant difference in numbers of male *vs.* female dolphins that were (1) removed long-term ($\geq$ 6 mo) following swimmer injury, (2) removed long-term for other reasons, or (3) never removed (Pearson Chi-square = 7.45, df = 2, $P < 0.024$; $n = 39$ dolphins; Table 6).

Further inspection identified a distinct age group of males—maturing and young adult males aged 9–16 yr—as those dolphins implicated in incidents of serious swimmer injury. Of a total of seven adult and maturing males participating in Swim programs since 1990 (when detailed record-keeping was initiated at NMFS), four were reported to seriously injure a swimmer, of which three were removed following the injury report (NMFS, unpublished). Of the three remaining adult and maturing males who have not been implicated in swimmer injury, two were young (5–8 yr) and one was older (18–21 yr) during this period. Serious swimmer injury and subsequent removal of male dolphins occurred in three of the four programs.

Female dolphins were also implicated in injuries to swimmers, but those incidents did not result in their removal from Swim programs (NMFS, unpublished). Long-term removals of females and immatures were associated with reproduction, illness, mortality, or replacement of show dolphins (NMFS, unpublished) and could not be shown to be related directly to Swim participation.

Staff response to escalation of risky activity—Escalation of high-risk and abrupt activity to the point that staff modified the normal Swim format occurred only in Not-Controlled programs. In one Swim session of one Not-Controlled program, a dolphin repeatedly breached near swimmers (abrupt activity), and trainers prematurely terminated the session. During 14% of sessions in the other Not-Controlled program, attendants modified the normal format in association with agonistic or sexual behavior performed by dolphins to swimmers. On these occasions, attendants requested a swimmer to leave the water (temporarily or

for the remainder of the session), entered the water themselves to escort swimmers to the dock, and/or made abrupt gestures or movements towards dolphins.

Comparison of Dolphin Behavior During Swims vs. Free Time

Incidence of behaviors designated as high-risk in the Swim context was compared with incidence of the same behaviors during free time to detect possible short-term effects of Swim participation on dolphin behavior.

Program 3 provided an opportunity to compare social behavior of the same dolphins under conditions of Controlled Swims, Not-Controlled Swims, and free time. The proportion of social time that dolphins were engaged in activity that was high-risk *vs.* not high-risk differed significantly from free time (11% high-risk) during Controlled Swims (0% high-risk; Fisher Exact $P = 0.000$, 2-tailed test) but not during Not-Controlled Swims (9% high-risk; Fisher Exact $P = 0.553$, 2-tailed test). Thus, the free-time social repertoire of dolphins was not modified during Not-Controlled Swims; whereas, high-risk behavior was absent from Controlled Swims even though such behavior was a normal component of the dolphins' free-time repertoire.

In all Controlled programs dolphins rarely engaged in agonistic behavior during Swims ($\leq$ 1% social time) even though such behavior was a normal part of the same dolphins' free-time social repertoire (3%–11% social time; Fig. 5a). In contrast, the proportion of social time that was agonistic was approximately equal when behavior of dolphins during Not-Controlled Swims was compared with their behavior during free time (5% *vs.* 5%, 9% *vs.* 11%; Fig. 5a).

In one Not-Controlled program, the proportion of social time that dolphins were engaged in sexual interactions was significantly different during Swims (17% social time) than during free time (4% social time; Fisher Exact $P = 0.000$, 2-tailed test; Fig. 5b). In contrast, dolphins in other programs never engaged in sexual behavior during Swims even though such behavior was a small but consistent part of their free-time social repertoire (3%–4% in two programs; Fig. 5b). That sexual behavior was rarely recorded during Swims or free time in Program 2 was an artifact of our study design—considerable sexual behavior occurred among those dolphins while they were in holding pools but our observations focussed on the behavior of dolphins while in the main pool.

Do Designated Refuges Provide a Choice for Dolphins?

Use of designated refuge areas—All programs were required by NMFS (1990, p.74) to provide a designated refuge area that dolphins, but not swimmers, may enter during Swims. In three programs a large portion of the main pool with unrestricted entry was designated as the refuge area; in Program 4, one or two enclosed pens with gate entries were designated as refuges.

Dolphins rarely entered refuge areas in any Controlled programs or in Not-Controlled Program 4 (Fig. 6). In contrast, during the Not-Controlled portion

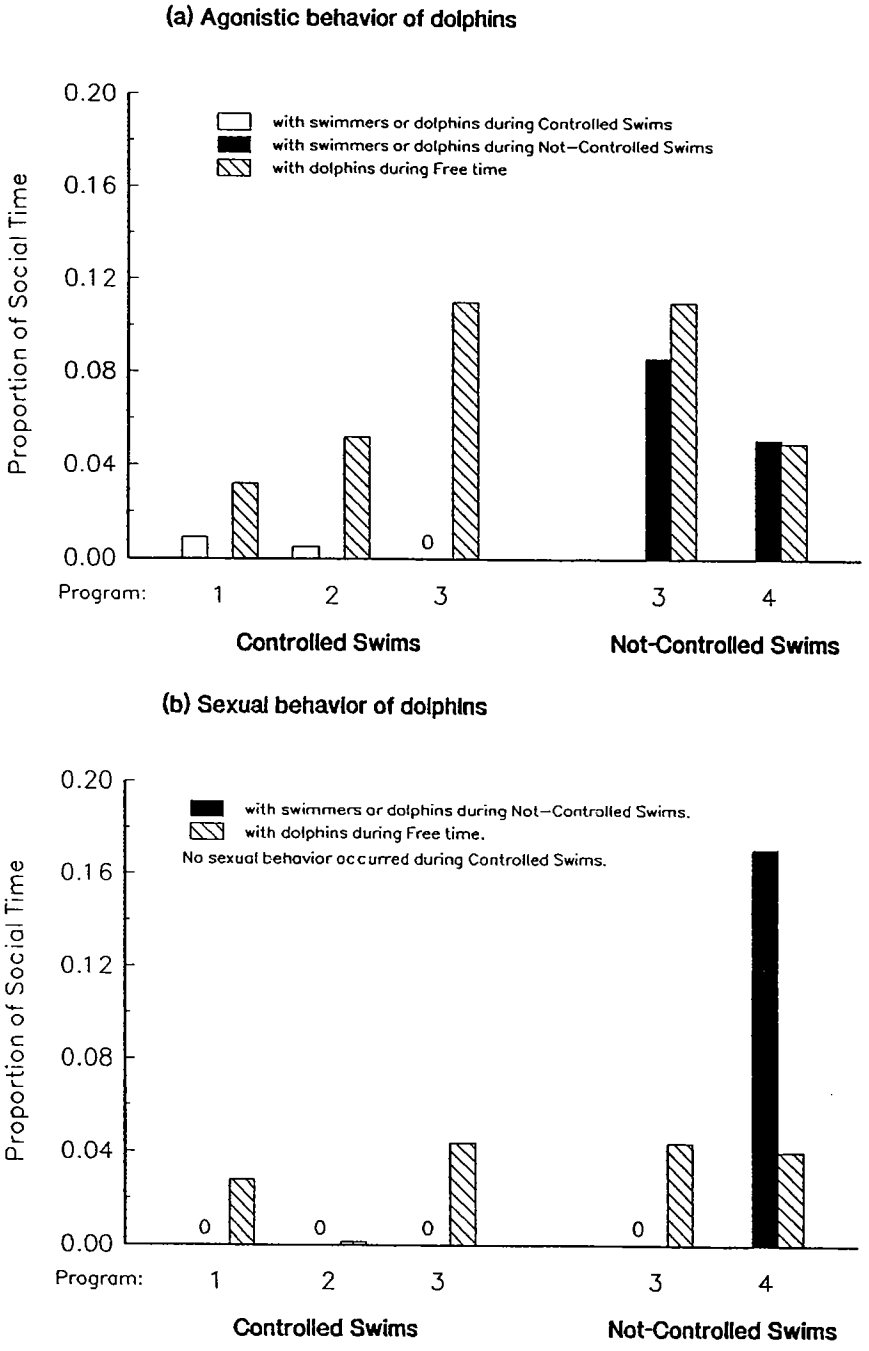

Figure 5. The proportion of social time that was agonistic (Fig. 5a) and sexual (Fig. 5b), comparing Controlled and/or Not-Controlled Swims with free time. Free-time values for Program 3 were repeated for comparison with Controlled and Not-Controlled Swims.

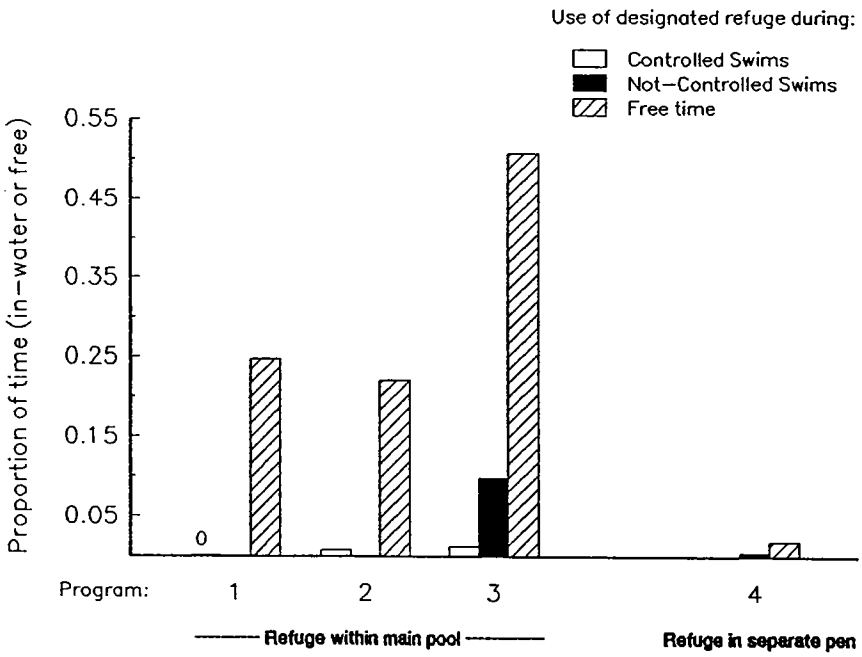

Figure 6. The proportion of in-water time during Controlled and Not-Controlled Swims *vs.* free time that dolphins spent in designated refuge areas, comparing refuge types.

of Program 3, dolphins entered the refuge area during 10% of in-water time (Fig. 6).

Interpretation of low-level usage of the refuge in most programs may be confounded by additional circumstances. First, during Swims in two programs, trainers periodically recalled dolphins from the refuge, an action likely to have reduced usage and effectiveness of the refuge. Second, Program 4 dolphins entered the refuge during only < 2% of free time (Fig. 6), and two dolphins were observed to enter these enclosures on one or fewer occasions. Thus, dolphins in this program were rarely observed to freely and voluntarily enter the refuge area, either during Swims or free time. In contrast, where the refuge was part of the main pool, dolphins frequently entered the refuge area during free time (22%–51%; Fig. 6).

Use of effective refuge—Designated refuges were the only choice of sanctuary from swimmers in Not-Controlled programs because swimmer movements were not restricted. However, in Controlled programs, dolphins were afforded an additional safeguard from unwanted swimmer contact because swimmers were not allowed to approach dolphins without trainer permission. Thus, during Controlled Swims, dolphins could avoid interaction with swimmers merely by staying away. Use of effective refuge was higher than use of the designated refuge in Program 3 (5% *vs.* 1% in-water time), and particularly in Program 2 (15% *vs.* 1%) where trainers sanctioned use of effective refuge more highly

than use of a designated space and typically did not recall dolphins who strayed from Swim activities.

Discussion

The many mythological and historical accounts of wild cetaceans seeking human company (reviewed in Lockyer 1990) predispose the public to expect friendly encounters with whales and dolphins. Although most descriptions of human encounters with wild cetaceans emphasize friendly relations, there are numerous examples of encounters that involve high-risk, injurious, and life-threatening behavior (*e.g.*, Lockyer 1978, Webb 1978, Lockyer and Morris 1986, Bloom 1991, St. John 1991, Shane *et al.* 1993), and in a recent encounter, a human swimmer died as a result of injuries inflicted by a wild dolphin (Associated Press, 9 December 1994). In this context, it comes as no surprise to find that human swimmers and dolphins also have risky encounters in some captive Swim-With-Dolphin settings. Specifically, this study showed that risky social interactions occurred at notable rates when encounters between dolphins and swimmers were not directly controlled by staff (Not-Controlled Swims). In contrast, activity that put dolphins or swimmers at risk rarely occurred when interactions between dolphins and humans were directly controlled by professional animal trainers (Controlled Swims). Comparison of interactions between dolphins and swimmers in one program, where the same dolphins and swimmers participated in both Swim types, revealed that direct control of interactions by trainers was a significant factor in determining the frequency of high-risk activity in captive Swim programs.

In this study high-risk activity was conservatively defined to include only dolphin-with-human activities that were generally agreed upon by marine mammal trainers and Swim program operators to be agonistic or sexual. Inclusion of dolphin-with-human sexual behavior as high-risk activity was a calculated decision based not on a moral stance but on quantitative analysis. We found that sexual behavior between dolphins and swimmers significantly co-occurred with agonistic behavior. This result suggests that dolphin-with-human sexual behavior is dangerous, no matter what the explanation for the association. In addition, it seems likely that the exaggerated rate of sexual activity during Swims relative to free time in one Not-Controlled program was attributable to some aspect of the human-dolphin encounter. Similar linkage of sexual and aggressive behavior has been suggested to occur when wild dolphins became habituated to interacting with humans (*e.g.*, Webb 1978, Lockyer and Morris 1986, Bloom 1991).

High-risk activity took two forms: swimmer-at-risk interactions in which dolphins were aggressive and/or sexual to swimmers, and dolphin-at-risk interactions in which swimmers' actions elicited submissive responses from dolphins. The predominant type of high-risk activity differed between the two Not-Controlled programs, perhaps as a result of opposite instructions given to swimmers. In one program, where swimmers were instructed to behave passively and allow dolphins to determine the nature of interactions, dolphins behaved in ways

that posed risks to swimmers. In the other program, where swimmers were encouraged to pursue interactions with dolphins, dolphins behaved submissively in response to swimmers' actions.

Although injurious consequences of high-risk activity were not observed in our study, we did observe risky activity in Not-Controlled programs that escalated until Swim sessions were terminated prematurely for one or all swimmers. Moreover, reports received by NMFS demonstrated that risky activity can escalate to the point of serious injury to swimmers. Although, historically, male dolphins were implicated in risky activity that resulted in swimmer injury, during our study when few males participated in Swims, we observed that female dolphins also engaged in high-risk activity with swimmers. Thus, swimming with dolphins clearly can pose a serious risk for swimmers when encounters are not directly controlled by trainers (Not-Controlled Swims); however, we cannot identify a single age/sex class of dolphins that poses this risk.

Do Swims also pose a risk for the dolphins? Results of this study indicate that dolphins may be at risk under certain conditions. When high-risk behavior escalates to the point of swimmer injury and dolphins must be removed from Swim programs, rejected dolphins may be at risk if adequate management plans are not made for their placement and care. Formulation of such plans is complicated by the fact that those dolphins historically implicated in human injuries and removed from Swim programs were maturing and young adult males who are typically not sought-after additions to captive cetacean collections. Adult and maturing males, whose relationships in the wild are typically tolerant of a select few males (Wells *et al.* 1987, Smolker *et al.* 1992) and antagonistic with most other males (Connor *et al.* 1992), require special conditions for peaceful integration into new social groups in captivity (*e.g.*, Caldwell *et al.* 1968, Amundin 1986).

When dolphins respond submissively to swimmers, dolphins are at risk in less obvious ways. Submissive behavior is traditionally viewed as an attempt by a subordinate to demonstrate how small, vulnerable, and non-threatening he or she is and thereby assuage or prevent aggression from a dominant. In many studies of primates it is submissive behavior (even in absence of aggression) that is used to identify dominant/subordinate status in a relationship (*e.g.*, Hausfater 1975, Sapolsky and Ray 1989). Submissive behavior has proven similarly effective as an indicator of dominance relations among bottlenose dolphins (Samuels *et al.* 1991, Samuels and Gifford, in preparation). In the present study actions of human swimmers—who were smaller, less-mobile, and presumably less-threatening than dolphins—caused dolphins to behave submissively, particularly in the Not-Controlled program where swimmers were permitted to pursue interactions with dolphins. Dolphin-to-human submission occurred during the same Not-Controlled program in which dolphins used the refuge area provided as an escape from swimmers, suggesting that dolphin-to-human submission is an expression of dolphin avoidance in response to some actions of swimmers. We conclude that, in a Not-Controlled format, trainers are unable to prevent intentional or inadvertent actions of swimmers that cause distress to dolphins.

There is growing evidence that, among social mammals, behavioral expression of submission may be a marker for physiological responses (*e.g.*, Keverne *et al.* 1982, Kaplan 1986, Sapolsky 1992). For example, in a long-term behavioral endocrinological study of wild male baboons (in which sampling methods were designed to minimize effects on subjects' endocrine levels), social subordinance among conspecifics was associated with unhealthy physiological measures, *e.g.*, high basal levels of glucocorticoids (Sapolsky and Ray 1989) and suppressed HDL-cholesterol concentrations (Sapolsky and Mott 1987). Sapolsky concludes that it is the stress of social subordinance that underlies these dominance-related physiological differences (Sapolsky and Mott 1987, Sapolsky 1992). Captive cetaceans that are subjected to constant psychological stress of subordination may also be vulnerable to significant health problems (Sweeney 1990). We cannot evaluate whether repeated submission by dolphins to human swimmers, as seen in one Not-Controlled program, is behaviorally or physiologically analogous to social subordinance to conspecifics. However, the behavioral endocrinological literature suggests that effects of subordinance may be more pervasive than the immediate outcomes of submissive interactions.

Dolphins are also at risk when they are unable to avoid unwanted interactions with swimmers. Designation of an area as off-limits to swimmers may not provide adequate sanctuary if dolphins perceive that area to be aversive or difficult to enter. In one program, although a designated refuge was provided, the dolphins were not observed to freely and voluntarily enter this area at any time, either during Swims or free time. Thus, it could not be assumed that the designated refuge area provided any sanctuary from swimmers. We could not identify which feature of this designated refuge was associated with avoidance by dolphins because the refuge differed from those of other programs in several respects, including smaller size, enclosed space, restricted entry *via* gates, and changeable location and shape. In other programs dolphins showed no aversion to refuge areas that were merely designated portions of the main pool.

The apparent choice afforded dolphins by a designated refuge area may be false if trainers habitually recall dolphins from the refuge during Swims and, especially, if dolphins receive the major portion of their diet as food rewards for interacting with swimmers. However, in one Controlled program, where trainers restricted movements of swimmers and permitted dolphins to stray from Swim activity, dolphins could create an effective refuge simply by moving away from swimmers. Moreover, in two programs, a changing daily roster of dolphin participation in Swims provided respites for dolphins who persisted in utilizing this effective refuge or were determined by staff to be uninterested in Swims.

We found no behavioral evidence that Controlled Swims with adequate refuge were deleterious for human swimmers or dolphins. Specifically, in Controlled Swims, trainers effectively eliminated behaviors that might put swimmers or dolphins at risk, even though the same behaviors were a normal component of the same dolphins' behavioral profiles when not participating in Swims with humans. Moreover, during Controlled Swims, we did not observe aberrant behaviors such as stereotypy, behavioral pathologies, or excessive manifestations of normal behavior (*e.g.*, Meyer-Holzapfel 1968, Greenwood 1977, Sweeney

1990, Gygax 1993). However, because of the limited scope of this study, we stop short of unconditionally concluding that Controlled Swims do not adversely affect well-being of participating dolphins.

The scope of this study was restricted, first and foremost, by the elementary level of knowledge about cetacean social behavior. The field of cetacean social behavior is currently in transition from a descriptive, natural history phase towards quantitative analyses of behavior. Despite an extensive literature on dolphin social behavior, few studies have employed quantitative sampling techniques like those used in this study. Consequently, the majority of what is known about social behavior of dolphins is of an anecdotal nature. In this study our interpretations were handicapped by the scarcity of quantitative analyses that evaluate the social functions of specified dolphin behaviors.

Full interpretation of this behavioral study was further restricted by absence of concomitant physiological measures. As previously suggested, subtle behaviors may indicate more pervasive physiological conditions. Physiological measures may be especially revealing if behavioral indicators of psychological stress are concealed as extensively as cetaceans mask visible symptoms of disease (Sweeney 1990).

Finally, results of this study cannot be used to draw conclusions about long-term effects of Swim participation on dolphin behavior. Urgency and logistical constraints precluded a study design that would properly evaluate long-term effects of Swims on dolphin behavior, *e.g.*, by tracking over several years the behavior of individual dolphins prior to and during participation in Swims, and/or by comparing results from the present study with comparable quantitative behavioral data from non-Swim dolphins (matched for age, sex, reproductive status, history, and living in zoo/aquarium environments and in the wild). It would be reasonable to compare results from the present study with a quantitative database of normal dolphin behavior; however, in absence of quantitative studies of cetacean behavior, such baseline behavioral information does not yet exist.

Caveats notwithstanding, this study serves important functions. Our results supplement and clarify recommendations by NMFS (1990) to better ensure safety and well-being of Swim dolphins. Our specific conclusions include:

(1) Direct control of dolphin-swimmer interactions by professional animal trainers effectively minimizes behavioral interactions that pose risks to dolphins and swimmers. Swim programs in which trainers do not directly control dolphin-swimmer interactions threaten the safety of swimmers and well-being of dolphins.

(2) Dolphins most likely to engage in high-risk activity resulting in swimmer injury have been adult and maturing males. The long-term well-being of male dolphins in Swim programs must be safeguarded by management plans that outline, specifically for males, programs of training, behavioral monitoring, and placement in other social groups in the event of rejection from Swims.

(3) Although, historically, it was male dolphins who were implicated in swimmer injuries, we observed that female dolphins also engaged in activity that put swimmers at risk. Thus, the risk to swimmers cannot be eliminated simply by removing male dolphins from Swim programs.

(4) Designation of a refuge area does not automatically guarantee dolphins

a means to avoid unwanted swimmer attention. Dolphins are afforded genuine choices to participate or not in Swims when trainers restrict swimmer movements, trainers permit dolphins to leave swimmers and/or to remain in refuge area, dolphin diet is not contingent on Swim participation, and dolphin participation in Swims can be rotated on a regular basis.

(5) Regular and systematic behavioral and biomedical monitoring, in addition to qualitative monitoring by trainers, is essential to ensure the well-being of dolphins who participate in Swim programs. This study illustrates effective use of quantitative behavioral sampling techniques for evaluation of management concerns, and more broadly, for a better understanding of cetacean behavior.

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CHAPTER 5. CONCLUSIONS AND FUTURE RESEARCH

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My thesis chapters focus on several different aspects of the social lives of bottlenose dolphins, but the primary take-home message is the same. Quantitative behavioral sampling methods used in complementary studies in captivity and in the wild move us toward a greater understanding of the social behavior and social relationships of cetaceans.

In compiling the history of research on the social behavior of cetaceans, I came to understand why it is that complementary captive studies and quantitative behavioral research techniques are not presently found in cetacean biology. I also realized that the historical reasons for these omissions are no longer necessarily valid. By demonstrating the value of studying social behavior in a captive setting, I hope to re-open the dialogue between captive and field research. By demonstrating the effectiveness of systematic sampling techniques, I hope to enlist other cetologists to use methods like these for measuring the social behavior of cetaceans.

However, despite the examples presented in this thesis of my own work and that of like-minded cetologists, many will continue to argue against the relevance of captive studies or against the feasibility of quantitative behavioral sampling methods in field research. And, indeed, there are behavioral issues that cannot be appropriately addressed in a captive setting, as there are species and field situations that are inhospitable to methods such as focal-animal sampling. Since many of my colleagues have already provided an exhaustive list of improper usages of these methods, I would make no contribution by adding to that list. Instead, I offer an extension of the common-sense

viewpoint of F. G. Wood (1986): not only are some captive situations more suitable than others for behavioral research, but in addition, some field settings are more appropriate than others for quantitative sampling techniques. My contribution will be to persuade my colleagues of the potential benefits of these techniques, and by doing so, to renew the discussion about when, where, and how these methods might best be applied.

To study the dominance relations of bottlenose dolphins at Brookfield Zoo, we adapted quantitative techniques from primate behavioral research. We found that the dolphins' dominance relationships were influenced by the gender of participants. Male dolphins were clearly and consistently dominant to females. Dominance relationships among female dolphins were age-ordered and stable, even though agonism among females occurred at low rates. In contrast, the two males had a changeable dominance relationship in which periods of stability and low-level agonism were interspersed with episodes of intense competition.

This study suggested that much may be learned in a captive setting about the social relationships of small cetaceans. Indeed, I would assert that certain aspects of the social behavior of difficult-to-see dolphins may be best studied in captivity where known individuals can be observed underwater and at close range on a daily basis, conditions that are rarely approximated in the wild. In addition, the captive setting may offer important benefits for studies of cetacean social behavior that include, for example, the ability of the investigator to manipulate the social group. In captive settings, it is possible to track how strangers establish their relationships, whereas first-time encounters in the wild are unlikely to be recognized as such. The captive setting may also provide a unique opportunity to decipher dominance relations of female dolphins for the very reason that typically low rates of interaction can be detected in captivity.

The relevance of captive studies, however, cannot be fully assessed or appreciated until more is known about the social behavior of free-ranging dolphins. In particular,

affirmation of the findings of this study awaits complementary studies of the social relationships of wild dolphins. Until such studies are conducted, we cannot assume that relationships observed among zoo dolphins are representative of those within communities of wild dolphins. In particular, the selective composition of the zoo group -- with females that were unrelated and only a single pair of males, one of whom was still maturing -- limited the conclusions that could be derived from the captive study. Moreover, it is possible that dominance relationships are less significant in the wild where animals spend more time searching for food and less time socializing, and where social exchange between individuals is more fluid, than is the case in a captive situation.

Nevertheless, observations made in a captive setting did enable us to generate plausible predictions about the behavior of wild dolphins, predictions that can be tested in field research using the technique developed in this zoo-based study. Future research will determine the role of (a) agonistic dominance within and between bonded subgroups of males, (b) polyadic agonistic interactions in determining dominance relationships, (c) body mass in determining the dominance relations among males and between males and females, (d) age *versus* kinship in determining dominance relations among females, and (e) social dominance in determining access to resources and reproductive success of bottlenose dolphins.

In our study of the association of wild juvenile bottlenose dolphins with their mothers, we found that juvenile female dolphins continued to associate with their mothers for several years following weaning. In contrast, juvenile sons rarely spent time with their mothers after independence even though they apparently remained in the same general area. Our preliminary results suggested that the broader social network of juvenile males may be quite different from that of their female counterparts. In particular, sex differences in the social associations of juvenile dolphins appeared to foreshadow their adult social networks.

This study sets the stage for a focused investigation of the social development of juvenile dolphins. Using focal-animal sampling, behavioral studies of juveniles of known-age, known-sex, and known-matrilineal group will determine how and when members of this life stage develop the social relationships that will be important in their adult lives. In a broader context, this study also lays the groundwork for investigating the significance of the juvenile life stage in a taxonomic group other than primates. Future research will need to focus on behavior, social associations, hormonal levels, and growth in order to refine delineators of the juvenile period, and to assess the relative importance of growth, learning, and investment in future social relationships during the juvenile life stage of bottlenose dolphins.

In our study of the behavior of dolphins in Swim-With-Dolphin programs, we found that direct trainer control of interactions between dolphins and human swimmers virtually eliminated high risk activity from the Swim context, and thereby diminished the potential for dolphin distress, swimmer injury, and rejection of dolphins from Swim programs due to swimmer injury. The specific findings of this study can be readily applied to the development of guidelines for captive Swim-With-Dolphin programs that seek to ameliorate the short-term effects of these programs on dolphin behavior and well-being. Additional research is needed, however, to evaluate long-term effects of Swim participation on dolphin behavior.

This study may have relevance beyond the management concern. By responding to an emotionally-charged issue with a quantitative methodology, we hope to have demonstrated to a wide audience the power of systematic behavioral research techniques for gaining an objective understanding of dolphin behavior. Perhaps we even succeeded in convincing some skeptics that behavioral studies of cetaceans can be conducted in a scientific manner.

Throughout this thesis, I have followed convention in referring to my study

animals as bottlenose dolphins (*Tursiops* spp.), regardless of differences in origin, body shape and size, and coloration. The taxonomic status of the genus *Tursiops* has long been in question, and I recently learned that the coastal forms found in waters near Western Australia and Sarasota, FL (formerly *Tursiops aduncus* and *Tursiops truncatus*, respectively) may be re-classified as separate genera (A. Hohn, personal communication). The shift in taxonomic classification is likely to result in a broader comparative perspective on social behavior and social organization than is typically the case in studies of cetaceans.

The inclusion of all forms as *Tursiops* has encouraged cetologists to look for commonalities of behavior. Some resemblances are to be expected among delphinids that share aspects of life histories and social structure, but these similarities might not have been pursued or revealed given a species-ist approach and a largely anecdotal methodology that emphasizes disparity over sameness. A broader perspective has enabled us to detect parallels in the social relationships of the Florida and Western Australia forms, including the stable, long-term relationships among certain males and among certain females that are obscured by the flexible composition of groups on a daily basis. With re-classification of these species, the focus is likely to shift in ways that illuminate which factors affect commonality *versus* variability in social behavior and social relations. For example, analysis of the similarities and differences in the social behavior, body size, and preferred associates of so-called bottlenose dolphins at Moray Firth, Sarasota, and Shark Bay is likely to lead to a better understanding of some of the factors that influence social structure and social behavior of these delphinids.

It seems clear from my historical review and from the studies that comprise my thesis that sophisticated studies of cetacean social behavior can now be accomplished. The life history background is better for cetaceans than for most other mammals. As a result of long-term studies, individual cetaceans can be studied within the context of demographic factors, familial relationships, and social associates. The logistical

difficulties of studying cetacean behavior are no worse than for a number of other mammals. It remains to overcome the historical obstacles, in particular, to recognize that social behavioral research is "hard science", to learn the techniques of systematic behavioral sampling, and to appreciate the contributions of complementary captive and field studies. The stage is set to embark on focused, quantitative studies of the social behavior of cetaceans.

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16. Abstract (Limit: 200 words)

Research on cetacean social behavior is in transition from descriptive natural history to quantitative analyses. To expedite this change, an intellectual history of the field is provided, from the early whaler-naturalists to oceanarium observations, whale carcass studies, pseudo-scientific inquiries into human-dolphin communication, and longterm field studies. Subsequent chapters illustrate use of systematic methodologies to better understand bottlenose dolphin social relations. Samuels and Gifford adapted a quantitative technique from primate behavioral research to study agonism among captive dolphins. Males were dominant to females; females had stable, age-ordered dominance relations; and two males had a changeable dominance relationship. Sex differences in dominance relations generated predictions about the behavior of wild dolphins that can be tested using this technique. Samuels, Richards and Mann investigated the association of wild juvenile dolphins with their mothers after weaning. Juvenile daughters continued to associate with their mothers, whereas juvenile sons rarely did so even though they remained in the same area as their mothers. Sex differences in juvenile association patterns appeared to foreshadow adult social networks. Samuels and Spradlin applied quantitative behavioral techniques to evaluate dolphin behavior in Swim-With-Dolphins programs. Two program types were defined by presence ("Controlled") or absence ("Not-Controlled") of explicit traner regulation of dolphin-with-human interactions. In "Not-Controlled" programs, the behavior of dolphins and humans threatened human safety and dolphin well-being, whereas "Controlled" programs effectively minimized behaviors that posed risk to dolphins or humans.

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